1997

The functional organization of the brain for mental imagery and image rotation: an electroencephalographic investigation

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The functional organization of the brain for mental imagery and image rotation; An electroencephalographic investigation

by

Harwant Singh Gill

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Co-majors: Neuroscience and Psychology

Major Professors: Michael W. O'Boyle and Srdija Jeftinija

Iowa State University

Ames, Iowa

1997

Graduate College

Iowa State University

This is to certify that the Doctoral dissertation of

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For the Graduate College

DEDICATION

I dedicate this work to the two loves of my life, Anja and Sebastian. Their love and "joix d'vivre" gave meaning to everything.

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ACKNOWLEDGMENTS

I would like to thank my parents, without whose upbringing I would never have developed a brain that never ceases to ask "why?", and my brother both of whose love and care have always had a special meaning for me. I will always be indebted to Michael O'Boyle who taught me everything I know about research and without whose support and friendship this dissertation would not have been possible. I thank Lloyd Avant and Alice Thieman whose friendship and support made Ames a nice place to be for me and my family. Last, but far from least I express my profound gratitude to my love and intellectual partner Anja, whose love, kindness and tolerance of me made this part of my life very special, in addition to making this work possible.

I would also like to thank all my assistants; Julie Hathaway-Nepple, Shawn Hoth, Tony Stewart and Kellie Clemmer, whose kind help contributed greatly to the success of these experiments. My only hope is that they had as much fun working with me, I had working with them.

I need to thank M.L. and D.K. for their gracious participation in these experiments as without their participation I would have not traveled as far or learned as much.

ABSTRACT

The intent of this dissertation was to utilize a set of cognitive tasks (that are visuospatial in nature) to investigate how multicomponent mental tasks are accomplished by the brain. Particular attention will be devoted to the processes that involve the generation of mental images and their rotation. The brain is known to approach complex tasks in an organized and planned manner which enables it to perform tasks of considerable cognitive complexity with relative ease. Here, an attempt has been made to define the functional brain system whose composite activity is required for successful performance on two such tasks: image generation and mental rotation.

MAPPING THE HIGHER COGNITIVE FUNCTIONS OF THE BRAIN

The answer to the question of how the brain subserves all the amazing cognitive functions we seem able to accomplish is, in spite of very intensive research, still elusive. Owing to progress in technology, we have at our disposal a variety of imaging techniques (e.g., Computerized Tomography (CT), Magnetic Resonance Imaging (MRI), Positron Emission Tomography (PET), Magnetoencephalography (MEG), Functional Magnetic Resonance Imaging (fMRI), Single Photon Emission Tomography (SPECT), regional cerebral blood flow (rCBF), etc.) which have provided us with perhaps more questions than answers. On the positive side, they have allowed us to peek at the human brain as it is working in real time, permitting minutes, sometimes even seconds, of mental activity to be manifest as a change in the image of the brain. On the negative side, not only are there technical problems with most of the aforementioned techniques, but there is also an inherent problem in that they are based on sets of assumptions which may or may not be correct (e.g., increased blood flow is thought to mean enhanced activation and localized involvement, but may potentially, relative to other brain regions, be indicative of inhibition instead) .

For example, one of the more popular imaging techniques is Positron Emission Tomography (PET). PET assumes that the region of the brain where an increase in glucose uptake occurs is most actively involved in the task being performed. Even if this should be the case, a further assumption, that the amount of glucose uptake is proportional to the level of activation is much more difficult to substantiate. For instance, if two hypothetical distinct cortical areas are activated during a given mental task, one could safely assume that there could/would be a detectable activational difference between the two. If one area is more

involved in performing a given component of the task, one might hypothesize that it would need less metabolic resources than another area which is conceivably struggling with the task (and thus utilizing more resources). Let us further imagine an experiment in which one subcomponent of the task is crucial for successful performance, and that the area struggling is doing so for a component which is only secondary in nature. If we follow the predominant (and highly intuitive) interpretation of PET results, one could draw the conclusion that our hypothetical task pivots on activation of the secondary area, which is in actuality performing only a minor portion of the task. Simultaneously, due to it's efficiency, the other area which does not require as much metabolic resource, might be assumed to be of secondary importance due to the lesser amount of radioactive tracer accumulated. Such interpretative issues are very difficult to resolve at our current level of factual knowledge of brain functioning, and they reappear in every instance when attempting to infer function from metabolic activity. In fact, Whitaker, Poeppel and Hochman (1997) have suggested that such confounds might be avoided by the use of converging independent data sources, such as those obtained from lesion studies.

Two other tools of brain investigation, Electroencephalography (EEG) and Magnetoencephalography (MEG), rely on the existence of recordable electrical waveforms measured at the surface of the scalp, which are somewhat physiologically indeterminate. In fact, Nunez (1995) goes so far as to call many of the proposed theories of physiologic basis for EEG pure tautology due to the complete lack of a realistic basis in physiology and anatomy.

He argues that any theory of EEG (and its interpretation) must identify the following:

- the neural tissue required to generate characteristic EEG frequencies,
- the physiologic time constants that support these particular frequencies
- the means by which spatial-temporal patterns change with physiologic state.

He proposes a qualitative model for EEG generation (see Figure 1) that encompasses the thalamus as the driver of cortex, and in interaction with it, as the receiver of inputs from a subcortical activating system that ultimately depends upon general sensory input.

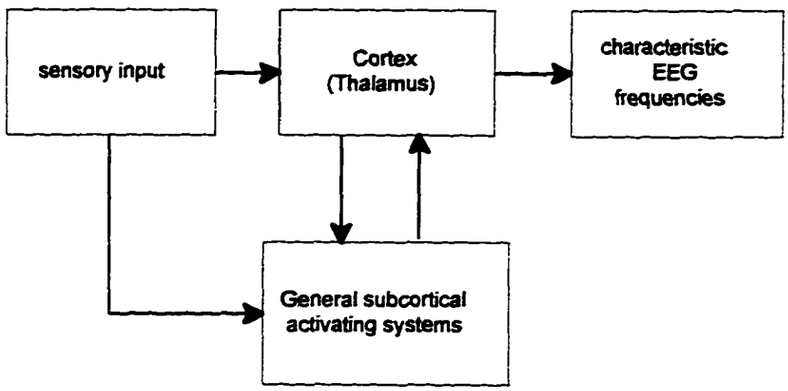


Figure 1: A qualitative model for EEG production (adapted from Nunez, 1995)

While it is still unclear what exactly are the origins of all components of the EEG, our understanding of the underlying physiological substrate has significantly advanced since the first recordings of electrical activity of the human brain were reported by Hans Berger (1929). Since then, a number of attempts have been made to find a consistent parameter of cortical activation that is clearly related to ongoing cognition. Almost all of the various electroencephalographic (EEG) components (e.g., wave frequencies, amplitudes, etc.) have

been investigated and, by the early seventies, it was generally accepted that the desynchronization of EEG with suppression of alpha waves (8-12 Hz) is the most consistent indicator of higher order mental activity (Butler, 1988).

For many years theories had suggested that the origin of alpha waves were thalamic "pacemakers" as the thalamus carries virtually all information to the cortex. However, Pilgreen (1995) has argued that the frequency of "alpha" that is used as an indicator of cognitive activity may primarily be due to cortical-cortical interactions, particularly in light of the fact that Lopes da Silva and van Leeuwen (1978) have demonstrated that thalamic input only minimally influences intracortical synchronicity of brainwaves.

Since the early seventies, the EEG has been used extensively to investigate higher-order cognition as it reveals underlying brain activity that cannot be monitored by other, more behaviorally oriented research techniques (Gevins, Zeitlin, Doyle, Yingling, Schaffer, Calloway and Yeager, 1979; Giannitrapani and Murri, 1988; Giannitrapani, 1985; Gevins, 1983; Gevins, Doyle, Schaeffer, Callaway and Yeager, 1980; Butler, 1988; Davidson and Ehrlichman, 1980; Galin and Ornstein, 1972; Cacciopo and Tassinary, 1990). Unfortunately, many EEG studies have methodological inconsistencies about them which may make their findings either inconclusive or difficult to interpret.

In an attempt to resolve such methodological problems Gevins, Zeitlin, Doyle, Schaeffer, Yingling, Callaway and Yeager (1979) have suggested several guidelines for studies that utilize EEG in the analysis of mental functions:

1. There should be no differences (or these should be minimal) between tasks in terms of stimulus properties.

2. Efferent activities should be kept the same across tasks.
3. In order to minimize EEG differences associated with task difficulty that could result in different effort between tasks, there should be minimal or no differences in performance related factors across conditions.
4. Behavioral validation should exist, indicating that the tasks were correctly performed during the time that the EEG recordings were made.
5. The EEG patterns of each hemisphere should be presented separately.
6. All extracerebral artifacts (e.g. muscle tension, eye-blinks, eye movements) should be rejected prior to analysis.

It appears that the debate over which of the aforementioned brain imaging techniques is best suited to examine cognitive processes remains open for discussion. However, some recent attempts have been made to relate the findings of brain activation pattern revealed by PET with EEG recordings. The results of recording using these two techniques are similar but not identical, as evidenced by two studies which utilized the same stimulus characteristics (subjects were required to imagine faces, spatial maps and colors) and measured accompanying brain activity using EEG (Uhl, Goldenberg, Lang, Lindinger, Steiner, and Deecke, 1990) and SPECT rCBF (Goldenberg, Podreka, Uhl, Steiner, Willmes, and Deecke, 1989).

These researchers found face imagery to be associated with left occipital activation although the effect was not large. Rather surprisingly, a left occipital activation was observed using EEG for map and color imagery processes, one that was not detected with

rCBF. It would appear from the findings of this study that the EEG was slightly ***more*** sensitive in detecting specialized brain involvement during task performance.

As compared to EEG, MEG is based on the recording of small magnetic fields induced by the current of brain electrical activity. As the currents inducing this magnetic field are extraordinarily small, the MEG technique depends upon the use of a Superconducting Quantum Interference Device (SQUID) which is immersed in liquid Helium (Naatanen, Ilmoniemi and Alho, 1994). Either by scanning with a single probe or covering the scalp with numerous probes, MEG produces "isocontour" maps which are three-dimensional representations of the different intensities of magnetic fields at different locations of the brain during mental performance. Because of the vectors of magnetic fields induced, MEG is most sensitive to activity in fissural cortex because the current there is parallel to the cortex, whereas it does not detect currents from pyramidal neurons which are positioned perpendicular to the skull (Naatanen, Ilmoniemi and Almo, 1994). In turn, the activity of those neurons that are found on the convexity of the gyrus is captured by EEG. This suggests that EEG and MEG are complementary, rather than mutually exclusive techniques. [For a detailed discussion of these and other brain imaging techniques see the excellent review of Springer and Deutch (1996) and Naatanen, Ilmoniemi and Almo (1994).]

For the above reasons, it appears that the EEG is an appropriate technique to apply in a study of localized brain processes when time locked events are not of primary interest. It is for this reason, in addition to its noninvasiveness, that it will be used in this study to investigate the brain locations subserving processes of mental imagery and mental rotation.

FUNCTIONAL SYSTEMS OF THE BRAIN

In the early seventies, Luria (1973) developed a theory to account for the organization of higher cortical functions. He stated that it is an oversimplification to ascribe particular mental functions to specific, singular areas of the cortex, and so too presumably, for a complex process like mental rotation. Although this may sound like common sense, this has not always been considered the case.

Using contemporary knowledge of the functions of distinct brain regions, Luria (1973) proposed a division of the brain into three functional units.

Unit One - *Arousal and Attention,*

Unit Two - *Sensory Input and Integration*, and

Unit Three - *Executive Planning and Organization.*

These three units would necessarily be activated during the performance of all mental tasks including generating an image and mentally rotating it. Each of the aforementioned units can be associated with a particular region(s) of the brain which together form a functional system.

The ***arousal and attention unit*** encompasses the function of the reticular formation. Fibers from the reticular formation ascend and terminate in a variety of structures (e.g., thalamus, caudate body, archicortex and neocortex). This structure appears to play a major role in the activation and regulation of cortical functions, and is under retrograde control of the cortex via descending pathways with, from Luria's standpoint, the most important connections coming from the frontal lobes.

The second, the ***sensory input and integration unit*** receives, encodes and sorts information. This unit occupies cortical areas posterior to the central fissure, encompassing visual, auditory and general sensory regions. Central to this unit (both functionally and anatomically) are the parietal lobes (Critchley, 1971), especially the tertiary zones of the inferior parietal lobule which have the capability of integrating excitation impulses coming from different sensory analyzers (Luria, 1973; Andersen, 1987).

Frontal lobe function is encompassed by a third, ***executive planning and organization unit***. These cortical areas have the capacity to synthesize information about external stimuli and, consequently, prepare for action by forming a program for efferent activity. The resulting behavior is also monitored by the frontal lobes making them uniquely capable of self monitoring. Through descending pathways, the frontal lobes have the means to mobilize subjacent structures, including the reticular formation and more importantly the thalamic nuclei (thus affecting the distribution of activational impulses coming from the reticular formation), in order to perform complex mental processes in a strategic and planned manner. In fact, the frontal lobes functional relationship with other regions of the brain has recently been demonstrated through studies in which manipulations of frontal cortex induced changes in delayed response task activity in the inferior temporal and parietal cortex. For example, the cooling process of prefrontal cortex simultaneously diminishes delay activity of neurons in the posterior parietal cortex (Goldman-Rakic and Chafee, 1994). Interestingly, in the inferior temporal regions, delay activity of neurons is disrupted by processing of intervening sensory inputs, while in the frontal cortex, this delayed activity is maintained as long as the animal is able to retain a memory trace of the original stimulus irrespective of the

intervening stimuli (Chelazzi, Miller, Lueschow and Desimone, 1993; Chelazzi, Miller, Duncan and Desimone, 1993; Miller, Li and Desimone, 1993). This finding suggest a unique capability of the frontal lobes to maintain a stimulus in working memory in spite of interrupting stimuli and circumstances).

Another, more recent finding that is likely to have an impact on the concept of a functional brain systems is the finding of the active electrochemical communication among neurons and glia cells (Parpura, Basarsky, Liu, Jeftinija, Jeftinija and Haydon, 1994). Apparently, glia cells, until now thought to serve merely a structural role and the role of the "milieu interior" maintainer, might have a part to play in modulating the activity of neurons (if not actually activating them). This finding has wide ranging implications (e.g., potential role of glia in long term memory storage) suggesting that a serious reconsideration of functional brain theories will be in order in the future.

Of particular interest to the present dissertation is the potential, by using our current knowledge of brain systems, identification of the functional system that mediates the higher order processes of image generation and mental rotation.

MENTAL IMAGERY

The ability to perceive things of amazing complexity in their physical absence is a capacity that is currently one of the most intensely investigated functions of the human brain. In the center of this ongoing mental imagery research is the issue of localization of function. Most researchers concern themselves with only the hemispheric contributions to the processes of mental image generation and their manipulations. It appears though, that the generation of mental images requires active contributions of both hemispheres, and an intricate interaction between the two.

Characteristics of Mental Imagery

Researchers like Finke (1989), Pylyshyn (1981) Kosslyn (1980;1983) and Farah (1984) propose that mental imagery comprises several cognitive subprocesses that, in the brain, might otherwise be dedicated to visual perception. Each of these researchers explains imagery processes in different terms, and each provides a somewhat different theory to account for the phenomenon.

Perhaps the most detailed theory of mental imagery is the one proposed by Kosslyn (1988). He begins by defining the medium in which images appear as a two-dimensional Euclidean space, referring to it as a "Visual Buffer". Cells in this visual buffer have spatial coordinates corresponding to those in the visual field. Thus, the activation of the array of cells (which is a consequence of some object being presented in the visual field) results in a pattern of activated cells that is isomorphic to the shape of the object provoking this activation. The stimulus object need not be visually perceived, but it's image can be generated from information about the object that are stored in long-term memory. Thus,

Kosslyn's (1988) aforementioned "visual buffer" is considered to be a short term memory structure in which representations of objects begin to fade virtually as soon as they are created. This is similar to the process that occurs on a TV screen; the image needs to be continuously refreshed by resampling either from information stored in long term memory or from impulses coming from the striate cortex. Moreover, Kosslyn suggests that there are size constraints within the "visual buffer". The grain of the medium defines how small an object may become and still be visible. On the other hand, a representation of an object can only be so large before the image "overflows" the scope of the mind's eye and parts of it become invisible (Kosslyn, 1988).

Once the image is encoded in the visual buffer, the pattern of activated cells can be further processed. This is accomplished by a series of processing modules, as proposed by Kosslyn (1988), which are discussed below. He makes a distinction between modules that use the image as input from those using long-term memory representations as the input. The former include such modules as FIND (i.e., examines and defines the image), RESOLUTION (i.e., improves clarity of the image), REGENERATE (i.e., prevents the fading of images when maintaining them over long period of time). He also proposes a group of modules that can reorganize depicted patterns, including ZOOM, PAN (i.e., the opposite of zoom), TRANSLATE (i.e., move), ROTATE, SCAN and PARSE (i.e., refreshes selected segments of objects thus creating new images). Processing modules that are active in the retrieval of images from long-term memory include PICTURE (i.e., recreating the appearance of objects from coordinate points stored in memory), PUT (i.e., coordinates separate encodings and fuses them into a single image) which is closely connected with FIND (i.e., used to "see"

where a currently encoded image belongs within a PICTURE). According to Kosslyn's theory, input from the eyes automatically proceeds and fills the visual buffer. An additional processing module named LOAD serves the purpose of maintaining the perceptual input from the eyes while simultaneously suppressing subsequent visual input. This module, therefore, is a counterpart of the PICTURE module with the difference being that the former receives input from the eyes, and the latter from long-term memory.

Using these modules, encoded images can be mentally transformed and then examined as if the output of these modules were actually perceived objects. For example, when describing the path to a certain location in a city, a series of visual representations are retrieved from long-term memory and moved to the visual buffer (without conscious effort), allowing one to mentally follow the path viewed in the mind's eye. Similarly, when asked to describe some object, most people will report creating an image of that object and then "looking" at it, and describing it "in absentia".

The Neuropsychology of Mental Imagery

Currently, there is neuropsychological evidence presented by Farah (Farah, 1985; 1988; Farah, Hammond, Levine and Calvanio, 1988) that representations of visual objects recreated from long-term memory traces share neural space with those that are result of direct retinal stimulation. In one of her experiments (Farah, 1985), participants were required to imagine a particular stimulus and after a brief period they were asked to identify a second flashed stimulus (Experiment 1). If the second stimulus flashed was identical to stimulus that the participants were imaging, the identification of the second stimulus was better when compared to the situation where the imagined object differed from the first. In Experiment 2

of the same study, stimuli were rotated and a match between imaged and flashed stimuli facilitated perception, but only if the flashed stimulus had the same spatial orientation as the imaged stimulus. Thus, Farah draws the conclusion that these interactions between imagery and perception imply a common locus of activity.

Recently, some PET studies have provided convincing evidence that mental images have topographical representations in the primary visual cortex (Kosslyn, Thompson, Kim and Alpert, 1995). In this study, Kosslyn et al. report consistent relationship between the size of the image with location of maximal PET activity, suggesting direct representation/mapping of the visual percept onto neural substrate. Additionally, they argue that stored visual information affects processing in the earliest visual areas, indicating that stored knowledge can fundamentally bias what we see (i.e., arguing for the top down processing influence on visual perception).

Kosslyn, Thompson, Kim and Alpert (1995), in their series of experiments, present an argument for different involvement of each of cerebral hemispheres during visual image generation and manipulation processes. In these studies, participants imaged letters into grids and/or brackets, as well as a dot above and below a line at a different set of distances. According to Kosslyn's theorizing, the former methodology encourages categorical (e.g., on/off, left/right, above/below) and the latter coordinate (e.g., metric distancing) image manipulations. He found that when coordinate image generation was the primary component of the task, the right hemisphere was superior in performance. Conversely, when categorical image generation was required, the left hemisphere outperforms the right. Farah, in her review of the imagery literature (1995) comments, quite appropriately, that it remains unclear

whether the right hemisphere superiority in performance of coordinate image generation is related to that hemisphere's known superiority in tasks requiring metric and spatial decision making, or to the image generation process itself. It might further be mentioned that one issue consistently avoided in this type of experimental work is the significant verbal/linguistic component in the categorical image generation task. When this linguistic component is present, it is impossible to ascertain if a left hemisphere superiority is related to the image generation process itself or rather to processing of verbally mediated stimuli that these manipulations require (i.e., left hemisphere is known to be superior in performance of tasks that are verbal/linguistic in nature).

Sergent has posed three basic neuropsychological questions (1990) which require answers within the domain of visual image generation;

1. What is the relation between imagery and perception and do they share common underlying structures?
2. Does image generation constitute an isolable process that can be selectively impaired by brain damage?
3. What are the neural substrates of image generation and the respective role of the cerebral hemispheres in this process?

Sergent (1990) defines the process of visual image generation as reactivation of information about an object stored in long term memory, one that reactivates the same visual experience of the object as during actual perception. She realized that the componential nature of any visual image generation task is important, and postulates the following steps that an individual must go through in order to perform a visual image generation task:

1. Understand the instructions.
2. Access information stored in the long-term memory based on the presented cue.
3. Possess the long-term memory store for the object to be imagined within the context of the task.
4. Be able to make the semantic connection between the task requirement and the object to be imagined.
5. Be able to generate the visual image.
6. Possess appropriate perceptual mechanisms for image visualization and inspection in order to make specific decisions and verbally report (depending on the response requirements).

Sergent admits that her assumptions and Farah's (1984) earlier componential breakdown of the image generation process may not have much in common with the actual functional organization of the brain, but correctly maintains that componential modeling brings rigor to experiments which otherwise would have difficulty in accounting for the myriad of findings about mental image generation.

In her extensive review of the empirical literature based on brain damaged patients, Sergent (1990) concludes that there is a lack of unequivocal findings defining the relative contribution of each cerebral hemisphere to the image generation process. In turn, Trojano and Grossi (1994) in their review of the literature based on investigation of defects in mental imagery without accompanying visual recognition impairments, concluded that mental imagery is indeed a disociable process which is mediated by the brain regions localized

posterior and to the left hemisphere. This essentially supports the contention of Farah (1984) and is consistent with Ehrlichman and Barrett's (1983) conclusion that there is no direct evidence to support the then prevalent notion that mental imagery is solely within the purview of the right cerebral hemisphere.

One attempt to utilize EEG to determine the brain activation patterns during an image generation task was a study conducted by Wells and Moore (1990). They found greater activation of the left hemisphere during the repetition of high imagery sentences as compared to activation levels during repetition of low imagery sentences. No difference in activation of the right hemisphere as a function of imagery content of the sentence was reported. Also, Marks, Uemura, Tatsuno and Imamura (1985) developed a topographical map of visual imagery utilizing EEG in which they found that, while imagining objects and scenes, participants have greater alpha suppression over the left (as compared to the right) occipital location.

Additionally, Farah provides support for her contention that the posterior left hemisphere mediates the process of mental imagery by citing several experimental findings (Farah, 1985, Farah, Gazzaniga, Holtzman, and Kosslyn, 1985, Farah, Hammond, Levine, and Calvanio, 1988) derived from a variety of neurophysiological methods (Farah and Peronnet, 1989; Farah, Peronnet, Gonon and Giard, 1988; Farah, Peronnet, Weisberg and Monheit, 1989). For example, Farah, Peronnet, Weisberg and Monheit (1989), using the same experimental procedure as Farah (1985) but adding electroencephalographic recordings during task performance, found that imaging of stimuli produced a change in the latency of the first negative component of the Event Related Potential (ERP) as recorded over the

occipital and posterior temporal regions (visual regions) of the scalp. This suggested that these regions are particularly involved in both visual perception and visual imaging. Additionally, this increased activation was particularly pronounced over the posterior left temporal location (significantly more so than on the right). Notably, this asymmetry was present only on trials where the imagined stimuli were induced by visually presented words. In trials where the image generation was induced by auditory presentation of a word, no asymmetry was noted though the same occipito-temporal involvement was again obtained.

It seems fair to say that a consensus of opinion has not been reached on whether mental imagery is mediated by the same cortical regions as those involved in actual visual perception, though Farah is one researcher who has been effective in promoting this viewpoint (e.g., Farah, Peronnet, Gonon and Giard, 1988).

Interestingly, Roland and Friberg (1985), had patients (scheduled for temporal lobe surgery) imagine, among other tasks, walking through their neighborhood turning to the right and to the left, alternatively. The difference in rCBF from baseline was measured and the main finding, besides activation of the superior prefrontal cortex across all conditions, was a significantly greater increase in rCBF in the visual association areas, superior occipital, posterior inferior temporal, and posterior superior parietal cortex during this route imaging task. Although the authors attribute the activation of the superior prefrontal cortex to the "organization of thinking", it is impossible to tell which of subcomponents might be related to all of the registered selective rCBF increases. (One problem in the design of this study was the fact that only one hemisphere was recorded making comparisons between left versus right hemisphere activation in any given participant impossible.) Irrespective of

methodological concerns, the Roland and Friberg (1985) study strongly implicates both the superior regions of parietal lobes and the inferior parietal lobule, as well as the superior prefrontal cortex as important in the image generation and manipulation processes.

Finally, Goldenberg, Podreka, Steiner and Willmes (1987) compared rCBF during a resting condition, with the memorization of words with or without imagery instructions. With imagery instructions, a leftward shift in rCBF was noted and was mostly due to the activation of the left frontal lobe. However, there was no significant hemispheric difference in blood flow for the imagery versus non-imagery tasks. Again, no appropriate controls for the linguistic nature of the task were employed, making it difficult to account for a potential confound of LH activation due to the verbal nature of the task as compared to actual image generation process *per se*.

As an aside, if one considers dreaming to be a very complex internal image generation process, it is important to note the findings of Greenberg and Farah (1986). In their extensive review of patients that experienced loss of the ability to dream due to brain damage, the authors found that the dreaming function appeared to be localized to the left hemisphere, a finding consistent with hemisphericity of voluntary image generation in an awake state as proposed by Farah and others.

MENTAL ROTATION

The present dissertation research is, in addition to the overall issue of mental imagery, also concerned with the process of mental rotation. This is probably the best known phenomenon involving mental image transformation (Cooper and Shepard, 1984).

A now classic study of mental rotation was conducted by Shepard and Metzler (1971). Their participants were presented pairs of line drawings of three-dimensional objects comprised of small cubes (see the Rotate condition of Figure 4). The objects comprising the pairs were sometimes identical but in different orientations, while at other times one of the objects was a mirror reflectance of the other. The stimuli were rotated either in the picture plane or in depth. Participants were required to verify whether or not the two objects were identical. Shepard and Metzler predicted that, in order to perform this task, participants would have to imagine rotating one shape into point of alignment with the other. Thus, they also predicted that the rotation process would take longer as the difference in angle of rotation between the shapes increased.

As hypothesized, the time it took to verify that the shapes were identical (or not) increased in direct proportion to the increase in number of degrees of rotation. A surprising outcome was obtained, however. When 180^0 degrees of rotation was exceeded, rotation times decreased, suggesting that participants changed the direction of the rotation, thus taking the shortest route to alignment. The linear correlation was equivalent for both picture plane and in depth rotations suggesting that participants were not merely rotating two-dimensional representations of three-dimensional objects (i.e. presented stimuli) but rather used 3-D mental images of the objects.

It is important to note that, for the mental rotation process to be performed correctly, a particular frame of reference must exist. This frame gives directionality to the rotation and provides a means of quantifying the degree of that rotation. Shepard and Hurwitz (1984) suggest that there are three possible frames of reference employed. The first, and probably the most often used, is one's own "egocentric frame" which is comprised of the dimensions up-down, front-back, and left-right with respect to one's own body. From this perspective one must differentiate between several possible points of reference: (1) the body as a whole, (2) the head only, and (3) the eyes alone. A second frame is defined by the same directional dimensions but the point of reference is some other object, hence the "object-centered frame". Here, objects can be either animate or inanimate and the directions of up-down, etc., follow the intrinsic characteristics of that object [e.g., if the object is a table, the flat surface is traditionally on the top (up) and the legs point down (bottom)]. The third frame of reference is the "environmental frame" which is defined by the directions up-down, north-south and east-west relative to a particular location on the surface of the earth.

These three frames of reference differ from each other with respect to their perceptual and cognitive availability. The directions up-down are most readily available for all three frames of reference, insofar as they are ultimately supported by constancy of the gravitational field which affects the senses, and also because most objects have very distinct top-bottom aspects; what is up for person A is most likely up for person B. The front-back dimension presents no problem in the egocentric frame of orientation, but it becomes more complicated in the object-centered frame. For example, front/back directionality is a source of major confusion in the context of mirror reversed information. Contrary to one's impression that it

is the left-right orientation that is reversed in the context of a mirror, it is in fact the front-back dimension that is actually reversed (Finke, 1989). Left is still on the left and right still on the right, but their relative position with regard to front-back direction has been reversed. Left-right directionality seems to be the least accessible frame of reference as there are no external field determinants which assist in this discrimination. A specific deficit in the ability to make left-right discrimination is part of the Gerstmann's syndrome which follows damage to the parietal regions (Critchley, 1971). While there probably are other internal determinants assisting in performance of left right discriminations, the lack of clear external field determinants still distinguishes the left-right reference frame from others. Moreover, most objects are bilaterally symmetrical which is of little help in left-right directional determinations as there are no particular features distinguishing left as opposed to the right side of an object.

Characteristic of Mental Rotation

A number of characteristics of the mental rotation process have been identified. One of the most important characteristics is the ***principle of transformational equivalence*** which posits that the actual physical transformations of objects and their imagined counterparts are identical. This principle enables one to make a number of predictions about performance during mental rotation such as the characteristics of the mental rotation process discussed below. Another characteristic of mental rotation is its ***holistic*** nature. Namely, mental rotation involves the imagined rotation of a complete object. This means that it is a process carried out in a holistic and not fragmented (piece by piece) fashion. Also, the imagined rotation is ***not dependent on the complexity*** of the object rotated since physical rotation is

possible even if the object is a very complex one (e.g., multi-pointed polygon versus a triangle).

The latter aspect of mental rotation were first demonstrated by Cooper (1975) who manipulated complexity of rotated patterns by virtue of varying the number of points on polygons used as visual stimuli. The finding was that rate of rotation did not differ between simple and complex objects. Further, that rotation is a holistic process was confirmed by Cooper and Podgorny (1976) in an experiment in which the rotated shape, again a pointed polygon, was slightly modified by changing the position of one of the vertices. If participants utilized only one feature of the object to perform mental rotation there would have been many trials on which a mistaken judgment would be made, since there was usually only one feature distinguishing the objects. Namely, any single feature may have easily been mistaken for another, while encoding of the gestalt of the object makes such mistakes much less likely. Since a high error rate was not in evidence, Cooper and Podgorny concluded that participants were utilizing the rotated shapes in their entirety during the mental rotation process.

Another important characteristic of mental rotation is ***continuity***. The supposition here is that rotation is not a series of static images succeeding each other in a stepwise manner but rather a smooth movement of a single image which passes through all the orientations from starting to finishing point (Cooper and Shepard, 1973; Cooper, 1976). For example, Cooper (1976) utilized participants who's individual rates of rotation had been established in previous mental rotation experiments. These participants were then shown random polygons (with which each participant was familiarized in six different positions in a

training session preceding the experiment), and they had to imagine rotating it in a clockwise direction. After a short delay, a test pattern was presented either in one of the familiar positions or in an intermediary, unfamiliar position. Cooper found that reaction times increased linearly with increases in departure of the test stimulus from where the imagined rotated stimulus would have been. This was also the case for both familiar and unfamiliar orientations of the test stimuli. The conclusion drawn was that mental rotation is at least approximately continuous, and that imagined rotation of objects takes them through at least some intermediate points along the rotational path.

The Neuropsychology of Mental Rotation

It is generally accepted that many forms of visuospatial processing are mediated by the right cerebral hemisphere (RH) (De Renzi, 1997; De Renzi and Faglioni, 1967; De Renzi, Faglioni and Villa, 1977). Researchers are, however, much less specific in addressing the question of which hemisphere mediates mental imagery and the mental rotation process *per se*. The latter is often assumed to be a right hemisphere function since it may be construed as within the general domain of visuospatial capacities. A number of studies, however, implicate a prominent contribution by the left cerebral hemisphere for aspects of spatial processing such as 3-dimensional maze learning (De Renzi, Faglioni and Villa, 1977), determination of line orientation (Mehta, Newcombe and Damasio, 1987), point localization in space (Ratcliff and Davis-Jones, 1972), and various forms of mental rotation (De Renzi and Faglioni, 1967; Mehta , Newcombe and Damasio, 1987; Mehta and Newcombe, 1991).

When reviewing visual half-field studies of mental rotation, one is confronted by a confusing array of results ranging from no hemispheric advantage, to either a LH or RH

superiority, depending upon the nature of the stimuli to be rotated (e.g., letters versus nonverbal forms), and other subtle task demands placed on the participant (e.g., concurrent memory loads (Corballis and Sidey, 1993) or 2-D versus 3-D mental rotations).

Moreover, authors sometimes report conflicting results within the same study. An example of such is Corballis and Sergent (1989). In this study, neurologically normal male and female college age participants and one commisurotomized patient were used. The commisurotomized patient underwent complete forebrain commisurotomy for intractable epilepsy at the age of 13. At the time of testing he was 35 years old. Rotated letters (F, P and R) were flashed to the participant's left or right visual hemifield, and were thus initially directed to the RH or LH. The flashed letter was either in a "normal" or "reflected" (i.e., mirror reversed) orientation, and participants were required to distinguish between the two possibilities. Reaction times (RT) and percent correct choices were recorded. Though the hemisphere of input effect was not statistically significant in RTs, normal participants made more errors when stimuli were presented to their RH (left hemifield). On the other hand, the LH was much faster in making correct decisions than the RH. The commisurotomized participant showed a statistically significant advantage for left hemifield (RH) trials where he made considerably fewer mistakes. In contrast to the normal sample, left hemifield (RH) presentations were responded to faster than right hemifield (LH) presentations. The authors attribute the LH superiority in the performance of the mental rotation task in normal participants to the fact that the stimuli used were rotated letters. Since the LH is specialized for processing of verbal material, this would be a likely source of the processing superiority.

Fischer and Pellegrino (1988) conducted a study similar to that of Corballis and Sergent (1989) but used both uppercase alphanumeric characters and Primary Mental Abilities (PMA) characters [i.e., eight two-dimensional figures from the PMA test (Thurstone, 1958)]. These stimuli were presented to each visual field, and participants were again required to identify whether they were identical or different, and to press a response key with either their left or right hand. The stimuli were rotated in the picture plane, and were either "normal" or "backward" (i.e., mirror reversed). Fisher and Pellegrino found an overall LH superiority of about 20 msec across all conditions in their latency data. Since this duration is comparable to reported corpus callosum transfer time (Hoptman and Davidson, 1994), the authors suggested that the delay in processing when stimuli are presented to the RH may be due to a transfer of information to the LH which, in fact, may perform the actual rotation. The LH also made significantly fewer errors with alphanumeric characters which, in their opinion, is consistent with a LH superiority based on the phonemic processing of linguistic stimuli.

Other studies address the question of hemispheric differences in mental rotation between the sexes. Van Strien and Bouma (1990) utilized unfamiliar shapes [Vanderplas and Garvin (1959) forms] as stimuli and presented them laterally in much the same manner as previous rotation studies. They found an overall LH superiority for mental rotation in females, while males showed no hemispheric differences. In this study, however, one cannot attribute the LH superiority to the alphanumeric character of the stimuli (as previously suggested by Corballis and Sergent, 1989) since the stimuli used have no obvious verbal

labels. This finding suggests that some component other than the linguistic nature of the stimuli contributes to the often reported LH advantage in mental rotation.

Burton, Wagner, Lim and Levy (1992) also reported visual field differences for the directionality of rotation. They found that clockwise rotations are performed faster in the left visual field (RH), while counterclockwise rotations were faster and more accurate in the right visual field (LH). In this experiment, geometric line drawings were used as stimuli and were presented visually in a lateralized manner. The authors speculate that clockwise rotation, when in the left hemifield, and counterclockwise rotation, when in the right hemifield, are both medially (i.e., towards body midline) directed rotations. However, the origin of this hemifield difference in directional rotation is still unclear. As already mentioned, a number of studies do not find hemispheric differences in performance of mental rotation in either direction (Cohen and Polich, 1989).

A somewhat perplexing set of results also comes from other more neurophysiological studies of mental rotation. For example, Deutsch, Bourbon, Papanicolau and Eisenberg (1988) reported greater RH than LH blood flow during rotation of Shepard and Metzler (1971) forms, while Ornstein, Johnstone, Heron and Swencionis (1980) found greater LH than RH parietal lobe activity using EEG techniques for the same stimulus materials. In the Deutsch, Bourbon, Papanicolau and Eisenberg (1988) study, however, the authors compared regional cerebral blood flow (using the ^{133}Xenon inhalation technique) in four brain regions (which did not correspond to the four brain lobes anatomically or functionally). The latter divisions were somewhat arbitrary as it was done in an attempt to separate association areas of the cortex from those involving primary sensory-motor functions. Curiously, three of the

four regions, as divided by authors, were comprised of both primary sensory-motor cortical areas and association areas and this overlapping makes it difficult to interpret their finding of greater right hemisphere involvement during mental rotation.

A different sort of problem is encountered in the study conducted by Ornstein, Johnstone, Heron and Swencionis (1980) as mentioned above, and is a difficulty often found in other mental rotation studies as well. The problem is that no control tasks for the component processes involved in mental rotation performance are employed. More specifically, participants are asked to perform a mental rotation task and physiological or chronometric measurements are taken. However, since mental rotation is comprised of many cognitive subcomponents, it is impossible to discern which of the subcomponents may be contributing most to the registered change in regional blood flow, the reduction in alpha power, or hemispheric performance superiority. An additional difficulty in the Ornstein, Johnstone, Heron and Swencionis (1980) study is that recordings were taken over the parietal and central regions, thus leaving possible activation of the prefrontal areas, temporal lobes and occipital lobes unmonitored.

Even though some researchers acknowledge the possibility that different hemispheres mediate different components of a mental rotation task, little attempt has been made to develop a technique that would isolate other subprocesses from mental rotation itself. One recent exception, however, is the work of Cohen, Kosslyn, Brieter, DiGirolamo, Thompson, Anderson, Bookheimer, Rosen and Belliveau (1996). In their study, functional magnetic resonance images (fMRI) were made while neurologically normal individuals mentally rotated pairs of Shepard and Metzler (1971) blocks into congruence, or in a comparison

condition, determined if a pair of three-dimensional (3-D) block stimuli were identical or mirror-reversed. In the latter, the authors contend that, because both stimuli of the pair appear in the same orientation, the comparison condition involves the same encoding, comparison and decision processes as the Shepard and Metzler (1971) task, but requires no mental rotation. They further reason that by subtracting the activational profiles generated during each of the two tasks, the cortical activity specifically associated with the process of mental rotation would be revealed in relative isolation from other subcomponents comprising the task.

In their study, Cohen et al. (1996) found consistent foci of activation during mental rotation in Brodmann areas (BA) 7a and 7b (sometimes spreading to BA 40), the middle frontal gyrus (BA 8) and some extrastriate activity, including BA 19 and 39 (essentially the brain regions corresponding to V5, and thought to mediate the processing of visual motion, see Zeki and Lamb, 1994). Moreover, differential activation of the frontal cortex (BA 9 and 46) was obtained, along with above threshold activity in the premotor cortex (BA 6). In more than half the subjects tested, hand somatosensory cortex (3-1-2) was engaged (as if the subjects were turning the stimuli with their hands), and in 50% of the participants, there was increased activation found at BA 18. There was little evidence of any asymmetrical lateralization of cortical activity. By way of summary, their data are consistent with the idea that mental rotation engages many of the same cortical regions required to track moving objects and to encode their spatial relations. And, the activational pattern they obtain is congruent with the notion that mental imagery engages the same cortical areas activated during direct visual perception.

One compromising aspect of the Cohen, et al, (1996) study, however, is that their comparison condition was not necessarily devoid of mental rotation as suggested. In fact, the mirror-reversed stimuli used in their comparison task seem to require that one member of the stimulus pair be rotated 180^0 (on its vertical axis in 3-D space to arrive at a match/no match decision (see Collins and Kimura, 1997; Cooper and Shepard, 1984). This fact may have affected the pattern of brain activation they attribute to mental rotation per se, as their resultant activational profile might reflect the combined activity of two different forms of mental rotation rather than isolating (by subtraction), the specific regions that mediate rotation as distinct from other component processes.

Attempts to create a mental rotation task in which control conditions have been designed in such a way as to test different components of a mental rotation task have been undertaken (O'Boyle and Gill, 1994; Gill, O'Boyle and Hathaway, submitted). The findings of these studies suggest an interactive and cooperative activation of different brain lobes in both hemispheres during mental rotation. For example, Gill and O'Boyle (1997) have developed a mental rotation task comprised of four experimental conditions. Each of these conditions was designed to tap into the various subcomponents of mental rotation. In each condition, the stimuli employed were modified Nebes (1971) circles (See Figure 2).

In the *Visual Encoding Component* (Figure 2a), the target stimulus was a circle, and the participant had to identify which of the five test circles had the same diameter. Distractors were 10 % and 20 % larger and smaller, respectively (this sizing of distractors was consistent across all trials and stimulus types). In this condition, the participant has to visually encode the stimuli, compare them and reach a match-no match decision indicating

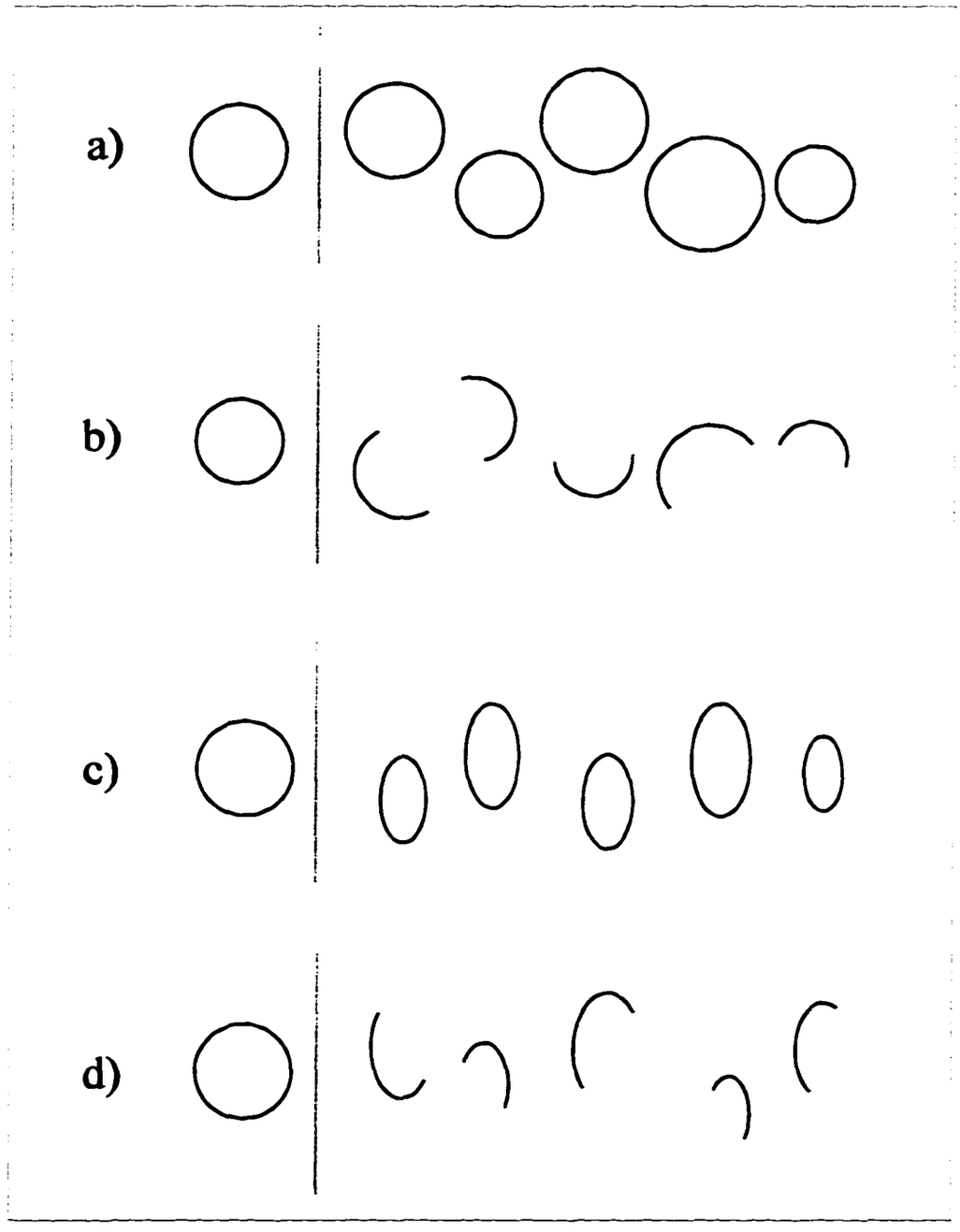


Figure 2: Example of test stimuli used in circles study: a) Visual Encoding; b) Image Generation; c) Mental Rotation; d) Image Generation and Mental Rotation (adapted from Gill and O'Boyle, 1997).

their choice by pointing it out to the experimenter. (This mode of response was followed in all conditions.)

In the *Image Generation Component* (Figure 2b) the target stimulus was a circle, but the test stimuli were arcs (180^0 segments of the respective circles of Condition a). The task required the participant to create a mental image of a circle using the presented arcs, and then decide which of the arcs matched the target circle in size.

In the *Mental Rotation Component* (Figure 2c) the target stimulus was again a circle, but the test stimuli were the circles described in the Condition a but were now rotated 45^0 on the vertical axis (i.e., they look like ellipses). Thus, the participant had to mentally rotate the test stimuli back into the same plane as the target circle in order to make a size comparison.

And, in the final, *Image Generation and Mental Rotation Component* (Figure 2d) the target was again a circle, but the test stimuli were the arcs described in Condition b except that now they were rotated 45^0 on their vertical axis. The participant was required to create a mental image of a circle using the presented arcs, rotate the imaged circle on it's vertical axis into the picture plane, and subsequently perform the size comparison (i.e., which of the five arcs matched the target circle). As can be seen in the first (Figure 2a) and third condition (Figure 2c), all the visual information necessary for successful completion of the task was contained in the stimulus.

The results of this study demonstrate a superiority of males as compared to females in performing three of the four visuospatial conditions, thus adding another task to the battery of spatial tests for which males are in some way more successful. Additionally, not only were

performance differences revealed, but different brain activation pattern between the sexes was also found.

By way of summary, the electrophysiological evidence from Gill and O'Boyle (1997) supports the hypothesis that the male brain is more lateralized/compartmentalized than the female brain. In the performance of three of the four conditions of their mental rotation test (Figure 2b, 2c, and 2d), males demonstrated the ability to perform each of the visuospatial tasks with minimal activation of cortex, save for the prominent and asymmetrical activation of the right frontal lobe. It is also interesting to note that males exhibited some non-significant inhibition of the left frontal lobe suggesting that its activation might have deleterious effect on performance.

The above activation pattern is particularly intriguing when compared with the brain activation pattern registered in females who manifested greater overall levels of activation which was bilaterally distributed across cortex. Specifically, activation was localized to both the right and left frontal and temporal lobes in all task conditions, with an increase in activation that paralleled the increase in task difficulty. If one considers the functional relevance of the frontal lobes, it is probable that one underlying cause for the less successful performance of females as compared to males was the symmetrical activation of the frontal regions. While the engagement of the right frontal lobe was expected given its known role in performance of many visuospatial tasks, the activation of the left frontal lobe in females, given its role in performance of verbal tasks, suggests that they may have engaged in some type of verbal strategy to perform the given task.

That there are sex differences in cognitive abilities has been often demonstrated (Hampson and Kimura, 1992; Halpern, 1986; Kimura, 1987; Hellige, 1993; O'Boyle and Benbow, 1990; O'Boyle and Hellige, 1989; O'Boyle and Hoff, 1987; O'Boyle, Hoff and Gill, 1995; Collins and Kimura, 1997; Deutsch and Halsey, 1991). Theories proposed to account for such differences between the sexes in spatial capabilities range from the purely biological to those maintaining that environmental and cultural influences during the crucial periods of development are at the cause (see Gill, 1995 for detailed discussion). The issue, however, remains unresolved.

INVESTIGATION OF THE FUNCTIONAL BRAIN SYSTEM SUBSERVING MENTAL ROTATION USING THE VANDENBURG AND KUSE MENTAL ROTATION TEST

In the present dissertation, EEG technique was utilized to investigate which brain locations subserve the component processes of mental image generation and rotation. By using a componential approach, where each of the subcomponents comprising the task are investigated in relative isolation, it was anticipated that the cooperative interaction among regions of the brain during mental rotation could be revealed.

One of the issues that presents a problem in attempting to localize mental rotation per se is the fact that it inherently includes the process of image generation. Namely, when an object is rotated in the "mind's eye" it automatically assumes a set of positions (during the course of rotation) that it does not physically assume in reality. This problem normally makes it impossible to differentiate which region of the brain subserves image generation as compared to the rotation component of the task. In order to address this issue, an individual with unilateral brain damage (e.g., a brain tumor) to one of the regions thought to play a part in rotation will be tested with a set of cognitive tasks that attempt to differentiate image generation from the rotation processes. This lesion/brain damage approach was most recently recommended by Whitaker, Poeppel and Hochman (1997).

Experiment 1

The first experiment utilized the EEG in an effort to localize the brain regions mediating each of the subcomponents comprising a prototypical mental rotation task and to shed further light on the relative contributions of the LH and RH to such processing.

Accordingly, twelve right-handed males performed the Vandenberg and Kuse (1978) test of mental rotation while alpha power (i.e., a known indicator of brain activation localized to the region beneath the electrode positioned on the scalp, see Gevins, Zeitlin, Doyle, Yingling, Schaffer, Calloway and Yeager, 1979; Giannitrapani and Murri, 1988; Giannitrapani, 1985; Cacioppo and Tassinary, 1990; Gevins, 1983; Gevins, Doyle, Schaeffer, Callaway and Yeager, 1980; Butler, 1988; Davidson and Ehrlichman, 1980; Galin and Ornstein, 1972) was monitored over the left and right frontal, temporal, parietal and occipital lobes.

Stimulus Materials

The hypothesized subcomponent processes of mental rotation are modeled in Figure 3 and were experimentally isolated by creating three task conditions: Encode, Match and Rotate (see Figure 4). All stimulus items were three-dimensional drawings of objects comprised of cubes (Shepard and Metzler, 1971). The first condition (Encode) was designed to monitor brain activity associated with basic level encoding, as the target and four test stimuli are all identical. The task here was to merely inspect each shape and to mentally note that they are all the same. In the second condition (Match), two of the four test stimuli match the target, but the subsequent comparison/decision process is relatively simple and the task does not require complex image generation or mental rotation. Thus, the Match condition theoretically indexes the combined neural activity of the encoding and comparison/decision subcomponents. The third condition (Rotate) is the actual mental rotation task (Vandenberg and Kuse, 1978) in which two of the four test stimuli match the target, however, the encoding, image generation, rotation and comparison/decision subcomponents are presumably now all interactively engaged.

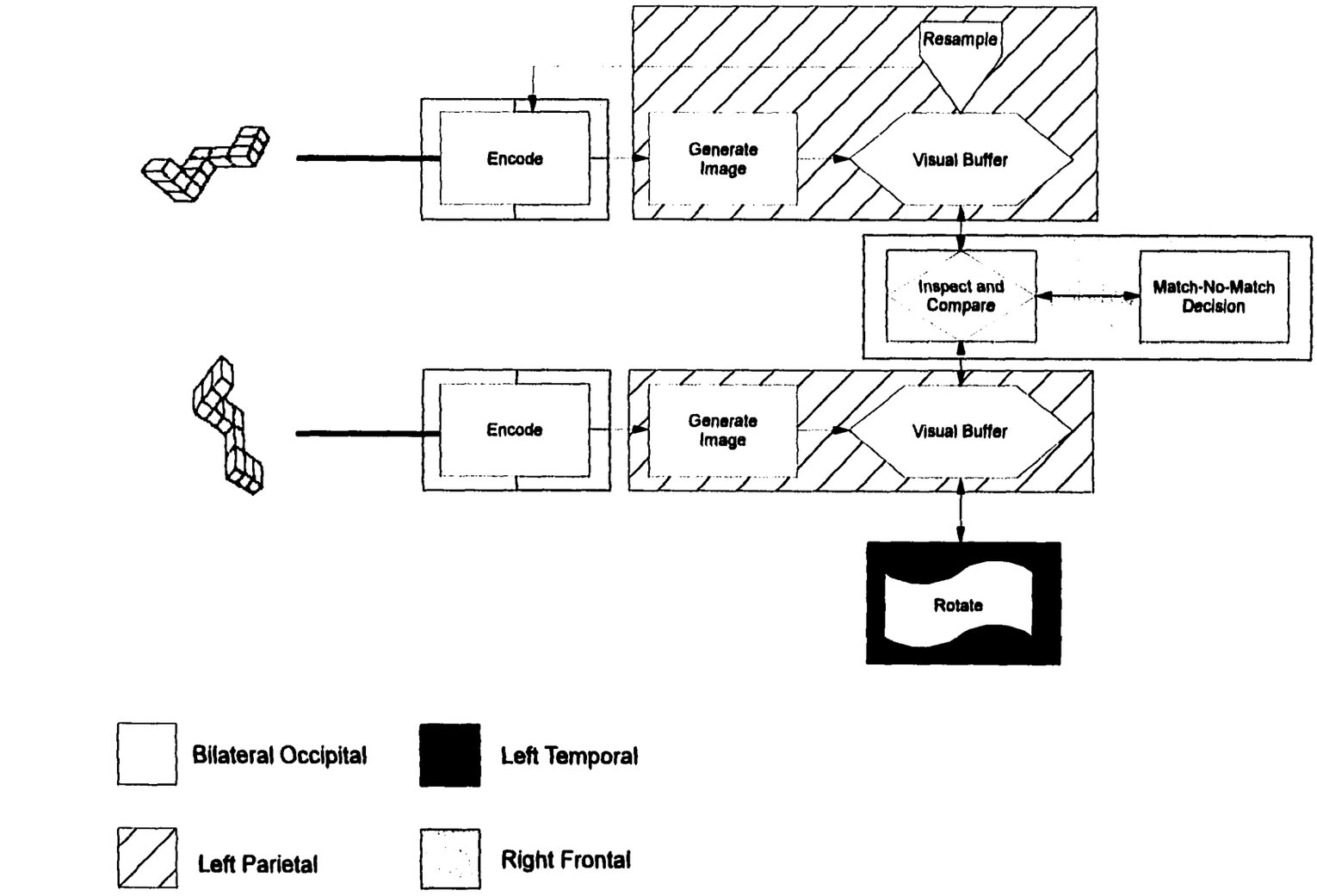


Figure 3: Model of Subcomponent Processes Comprising Mental Rotation

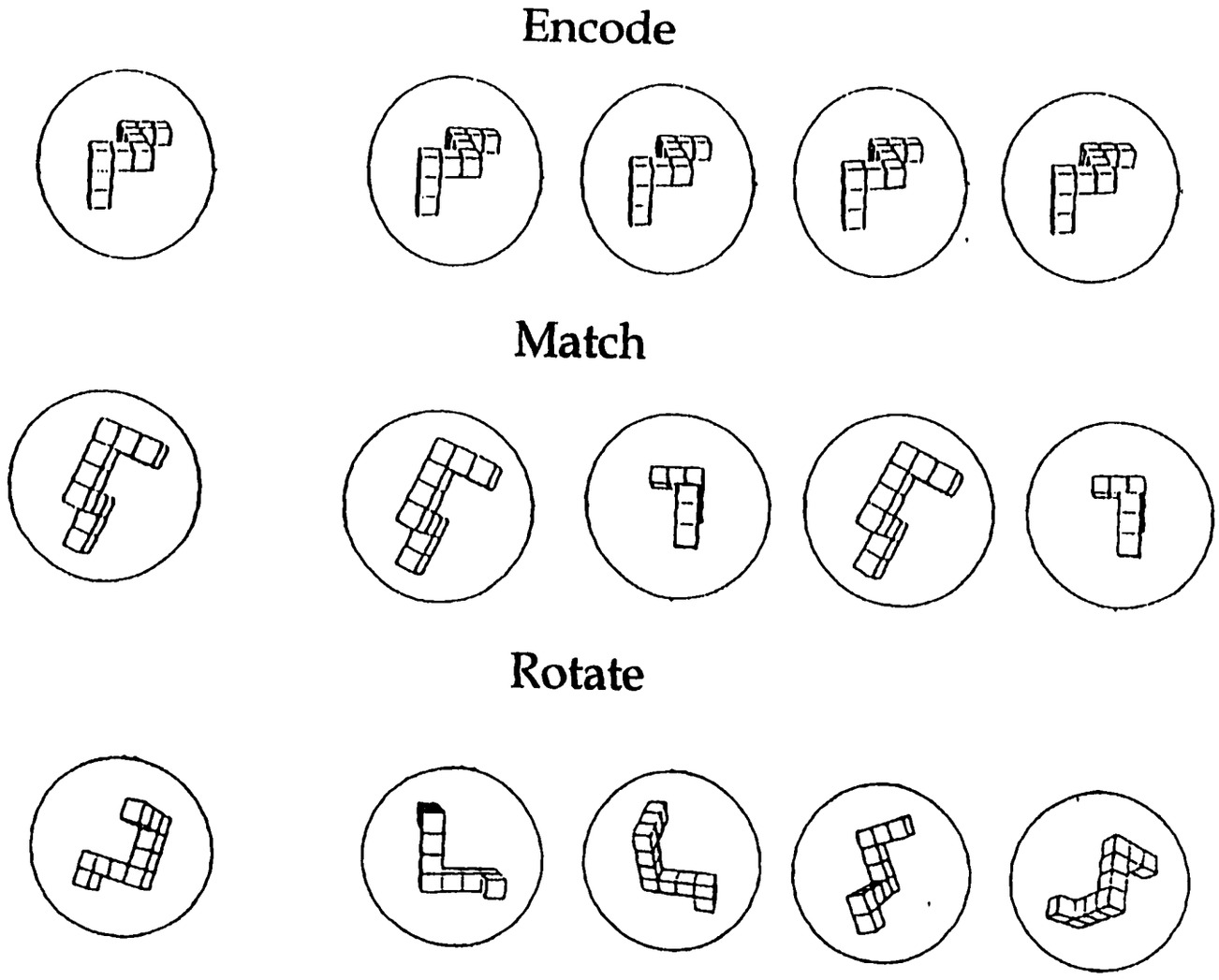


Figure 4: The Three Experimental Task Conditions

Participants and Procedure

Twelve right-handed male undergraduates at Iowa State University (aged 18-22 years) participated in the study. Right hand preference (which is hypothesized to reflect a strongly lateralized organization of the brain (as in Bryden, 1982) was determined using a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). Prior to the experiment, participants read a set of instructions and were given three paper and pencil mental rotation items for practice. They were then seated in a reclining chair in an electrically shielded and sound attenuated chamber.

Design

During the experiment, all participants received four blocks of trials (Baseline, Encode, Match, and Rotate). Baseline trials consisted of 5 blank slides with a 4 sec recording epoch; The Encode and Match conditions consisted of 10 slides each, with a 10 sec recording epoch; the Rotate condition was comprised of 20 slides with a 40 sec epoch. In the Match and Rotate conditions (each trial) subjects were required to identify which two of the four distractors could be mentally rotated into congruity with the target item.

Baseline slides were always presented first followed by the three blocks of task conditions counterbalanced in a Latin Square. All stimuli were presented on an off-white screen at a viewing distance of 1.5m using a Kodak Carousel projector, and participants were required to indicate their choices using a hand-held pointer.

An eight channel Grass electroencephalograph and an ECI electrode cap (Blom and Anneveldt, 1982) were used to monitor alpha activity at sites Fp1, Fp2, T3, T4, P3, P4, O1 and O2 (Jasper, 1958). Linked earlobes (A1 + A2) served as reference leads and electrode

impedance was maintained below 10kΩ. The eight channels were calibrated to a standard of 50μV and EEG was digitized on-line by microcomputer at 100 samples per sec using Unkelscope® data acquisition software. Eye blinks were edited from the recording, and alpha waves isolated using an 8-12 Hz bandpass filter. Power spectral analyses were performed on the resulting 360 filtered recordings [(2 hemisphere x 4 locations) x (5 baseline + 10 Encode + 10 Match + 20 MRT trials)].

Results and Discussion

Behavioral Data

Participants were awarded one point for each test stimulus correctly matched to the target. In the Encode condition there was no matching required. In the Match condition participants were 100% accurate, and in the Rotate condition accuracy was significantly reduced to 84% [$t(11) = -6.07$, $p<.0001$, SE=2.70]. This reduction in accuracy supports the notion that adding more subcomponents to the task increases cognitive complexity and thus task difficulty.

Electrophysiological Data

A one-way Analysis of Variance (ANOVA) on the mean alpha power values for each task condition (Baseline, Encode, Match, Rotate) proved to be significant [$F(3,380)=92.62$, $p<.00001$] with a post-hoc Tukey's HSD test ($p<.05$) indicating an increase in brain activation as the task conditions became cognitively more demanding (see Figure 5). Specifically, the Encode condition and the Match condition produced more activation than Baseline (i.e., less alpha power). Although in the expected direction, the Encode condition and the Match condition did not reliably differ from one another in level of activation.

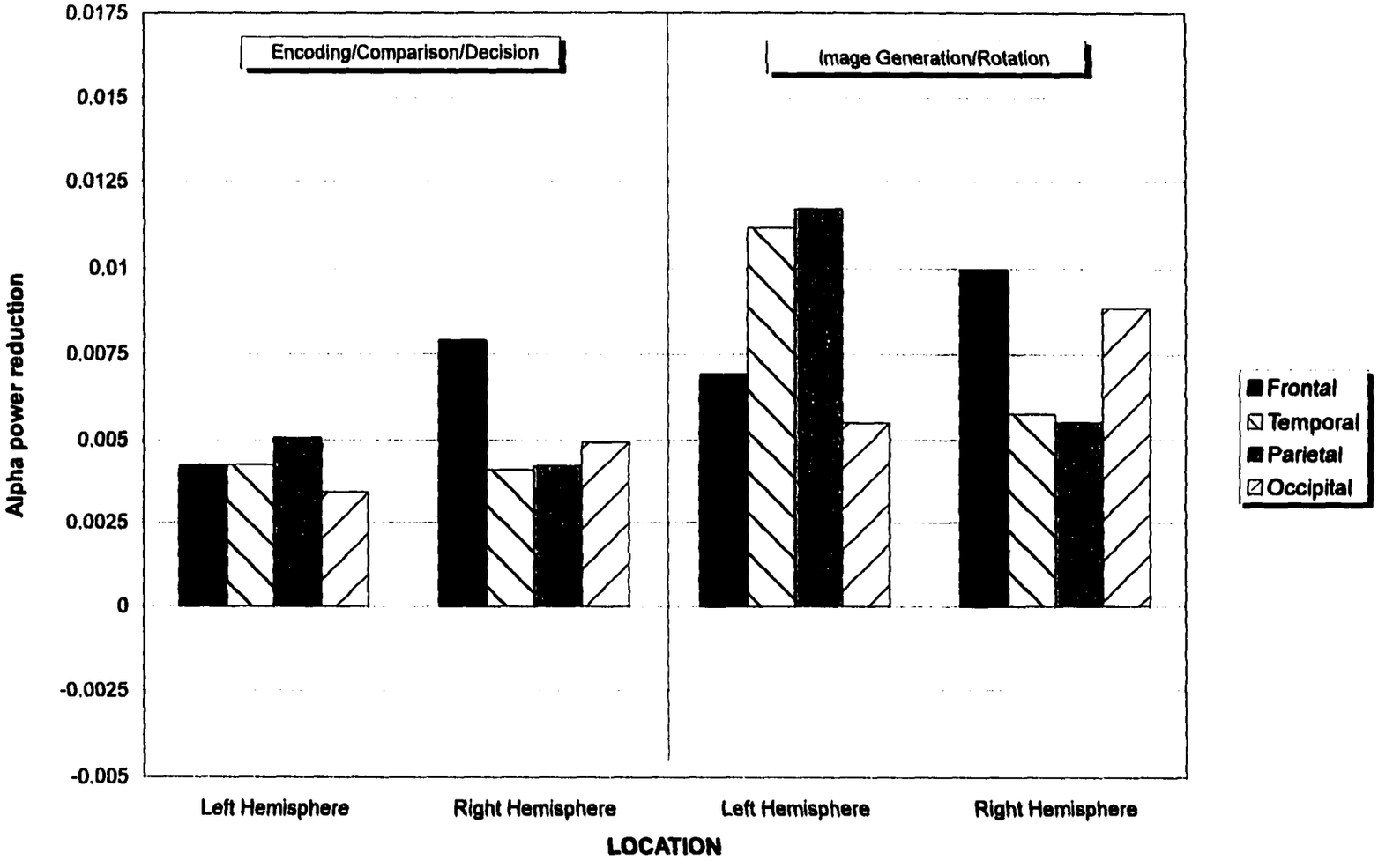


Figure 5: Alpha Power Reductions (V^2/Hz) for Encoding/Comparison/Decision and Image Generation/Rotation in Neurologically Normal Individuals

Apparently, the rather minimal comparison/decision requirement of the Match condition was insufficiently taxing to induce additional brain activation. As anticipated, the Rotate condition produced a significantly greater amount of brain activity than the Baseline, Encode and Match conditions.

Because each of the three task conditions cognitively builds upon the other (due to the systematic inclusion of additional subcomponents required for performance), using a subtractive logic should provide insight into the brain regions that may be selectively activated during each of the processing stages depicted earlier in Figure 3. In keeping with this logic, a series of analyses were conducted to evaluate activational changes across the cortex corresponding to performance during each of the task conditions. Thus, mean alpha power reductions (i.e., changes in brain activation level) associated with basic level encoding (Baseline - Encode), encoding plus comparison/decision processes (Baseline - Match), and encoding plus image generation, rotation and comparison/decision processes (Baseline - Rotate) were each submitted to a 3 Task (Encode, Match, Rotate) x 2 Hemisphere (left, right) x 4 Location (frontal, temporal, parietal, occipital) repeated measures ANOVA.

The results of this analysis revealed significant main effects for Task [$F(2,264)=221.85$, $p<.0001$], with a post-hoc Tukey's HSD test ($p<.05$) showing that the Rotate condition induced a higher level of activation than the Encode and Match conditions (with the latter two not reliably different from one another), and a main effect for Location [$F(3,264)=7.58$, $p<.002$], with post-hoc testing indicating that the frontal lobes were significantly more active than the temporal and occipital lobes (but not reliably different from the parietal regions). The main effect of Hemisphere was not significant. Also, the

Hemisphere x Location interaction was statistically reliable [$F(3,264)=24.78$, $p<0.0001$] with post-hoc analysis showing that the right frontal region was more active than any other brain site ($p<0.01$), with the exception of the left parietal area. Moreover, it was revealed that the left parietal region (though not significantly different from the right frontal, left temporal and the right occipital areas) was reliably more active than all remaining brain sites ($p<0.05$).

Of particular importance, however, was the finding of a significant Task x Hemisphere x Location interaction [$F(6,264)=5.66$, $p<0.0001$] indicating that performance during each of the three task conditions selectively engaged different brain regions. Post-hoc decomposition of this three-way interaction was accomplished by performing separate 2 Hemisphere x 4 Location repeated measures ANOVA on the activation patterns produced for the Encode/Match conditions combined (as they did not differ from one another in the preliminary one-way ANOVA) and for the Rotate condition.

Encoding and Comparison/Decision Processes

To identify the brain areas most active during the encoding and the comparison/decision subprocesses, mean reductions in alpha power for the combined Encode and Match conditions were subtracted from Baseline activity. The resultant 2 Hemisphere x 4 Location repeated measures ANOVA performed on these reductions revealed no significant main effects, however, the two-way interaction was statistically reliable [$F(3,88)=2.83$; $p<.043$]. A Post-hoc Tukey's HSD test ($p<.05$) indicated that the right frontal lobe was more active than any other brain site, a finding which suggests that this region plays the major role in the encoding and comparison/decision subcomponents of the task (see the left panel of Figure 5).

Image Generation and Rotation Processes

To reveal the brain areas most active during image generation and rotation processes in relative isolation from the activation associated with encoding and comparison/decision processes, mean alpha power reductions obtained for the Rotate condition (image generation and rotation) were subtracted from those associated with the combined Encode condition (basic level encoding) and Match condition (encoding plus comparison/decision). The resultant 2 Hemisphere x 4 Location repeated measures ANOVA revealed a main effect for Hemisphere [$F(1,88)=14.79$; $p<.0002$] and for Location [$F(3,88)=3.81$; $p<.012$]. These main effects, however, were tempered by a significant two-way interaction between these factors [$F(3,88)=57.17$; $p<.0001$]. Post-hoc evaluation using a Tukey's HSD test ($p<.05$) revealed that the most active sites during image generation and rotation were the temporal and parietal lobes of the LH, with enhanced activation also manifest at the right frontal and occipital lobes (see the right panel of Figure 5). This pattern suggests that the left temporal and parietal areas are particularly engaged during the internal generation of complex mental images and the subsequent rotation process required to reach a match/no-match decision. By way of speculation, it may be that the increased activation of the right occipital region is related to the hypothesized resampling of the visual input to refresh the internally generated image when performing this task (see this subcomponent process as depicted in Figure 3).

The cortical areas selectively engaged during each subcomponent process of the mental rotation process are superimposed on Figure 3. This model was created by incorporating fundamental notions about mental rotation as previously expressed by others (e.g., Cohen, et al., 1996; Farah, 1984, 1986, 1995; Farah and Ratcliff, 1994; Farah, et al.,

1988; Kosslyn, 1980, 1983, 1988, 1994; Kosslyn, et al., 1995; Gill and O'Boyle, 1997; O'Boyle and Gill, 1994), and is supplemented by findings of Experiment 1. Although the implications of these findings will be addressed in detail in the General Discussion, what was apparent from Experiment 1 is that several brain locations actively participated in the performance of the mental rotation task, and thus forming a functional system encompassing a number of cortical regions of both hemispheres.

Experiment 2 (A Case Study)

The findings of the first experiment suggested that the right frontal lobe mediates basic level encoding and comparison/decision processes, while the left temporal and parietal lobes are crucial for complex image generation and rotation. However, it was impossible to determine from these data alone which of the later two areas may specifically mediate the subcomponent of primary interest in this study, namely mental rotation, since it always includes the mental image generation subcomponent. Previous neuropsychological research has linked temporal and/or parietal lobe damage to various disorders of spatial processing, including constructional apraxia, visuospatial agnosia and the formation and manipulation of mental images (for reviews see, Kolb and Whishaw, 1996; McCarthy and Warrington, 1990).

Thus, in order to investigate the brain region mediating the actual rotation of a mental image, a patient with focalized damage to the left temporal lobe was tested. By juxtaposing the performance of this patient with that of the neurologically intact individuals tested in Exp. 1, the cortical area subserving the rotation process might specifically be revealed.

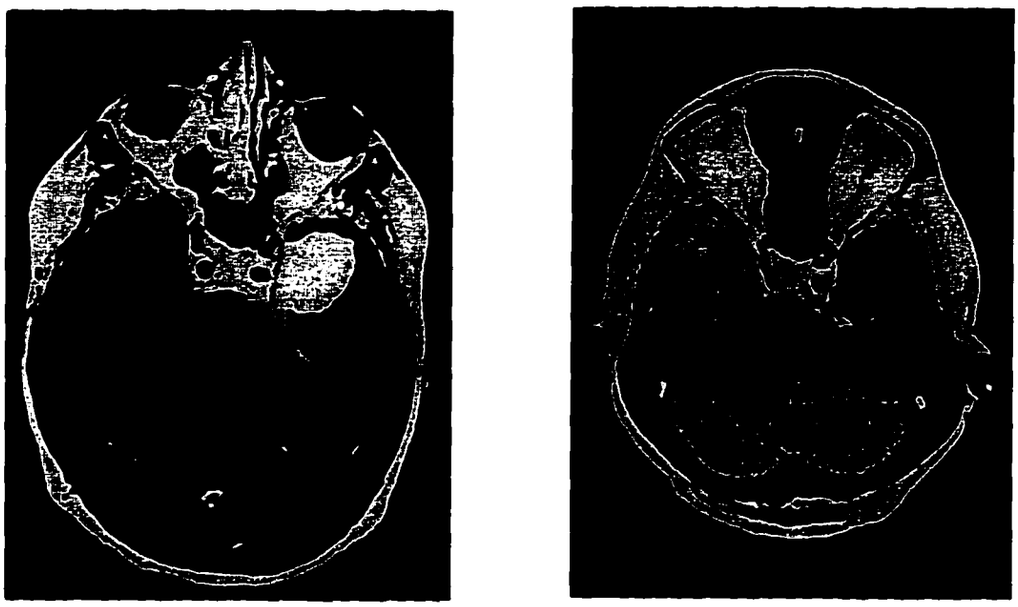
Participant

Patient M.L. is a 54 year-old female who has undergone surgical removal of a tumor, specifically a left side sphenoido-tentorial meningeoma, measuring 3 x 3 x 2 cm (Figure 6a).

The surgical procedure included the resection of approximately $1cm^3$ of the damaged tip of the left temporal lobe (Figure 6b). Her recovery has been sufficiently successful to allow M.L. to attend college on a part-time basis.

Materials and Procedure

M.L. performed each of the task conditions (Encode, Match, Rotate) as described in Experiment 1 to determine if she was able to generate internal images and mentally rotate



(a) Preoperative (b) Postoperative

Figure 6: Pre- and Post-operative MRI scans of Patient M.L. Note that the left hemisphere is imaged on the right and the tumor (in 6a) appears as a light gray circular shadow.

them despite damage to her left temporal lobe. In addition (though not with accompanying EEG recordings), M.L. was tested on the Object Assembly and Block Design subtests of the WAIS-R. The latter were administered to measure her general level of visuospatial ability and to index her capacity to generate images without the necessity for mental rotation.

Note that in the Object Assembly task the patient is asked to arrange scrambled parts of an object to match a target whole. No mental rotation is required since the patient is able to physically manipulate the pieces to check for orientation and completeness of form. On the other hand, generation of an internal target image, according to which pieces are to be manipulated is necessary for successful completion. In the Block Design task the patient is asked to arrange three dimensional blocks with red and white quarters, adjusting them to match a specified target pattern. Again, image generation of a target block design pattern is necessary, while no mental rotation is required.

Design

The design of Experiment 2 matched that described for Experiment 1.

Results and Discussion

Behavioral Data

For Object Assembly, M.L. performed in the average range (32 Raw Score, 11 Scaled Score, 65th Percentile), and on the Block Design task she also performed in the average range (28 Raw Score, 11 Scaled Score, 65th Percentile). In neither case were there any apparent visual or motor manipulation difficulties. However, on the Vandenberg and Kuse (1978) Mental Rotation Test (the Rotate condition of Experiment 1), M.L. was correct only 57% of the time, a level of accuracy considerably lower than that of the neurologically

intact participants tested, and sharply contrasts with the 100% accuracy she obtained in the Match condition where both encoding and comparison/decision processes are required but mental rotation is not.

When taken in conjunction with the findings of Experiment 1, these results, along with other reports that patients with intact left parietal lobes (but damaged left temporal lobes) are able to utilize imagery techniques for memory rehabilitation (Jones, 1974, Jones-Gotman and Milner, 1978), suggest that the left parietal area is essential for image generation, but it is the left temporal region that is crucial for actual rotation as this damage selectively impairs M.L.'s mental rotation capacity.

Electrophysiological Data

Although based solely upon recordings obtained from a single brain-damaged patient, and are thus to be viewed with caution, there are some activation patterns exhibited by M.L. that are worth noting. As can be seen in Figure 7, for the Encode condition (basic level encoding) and the Match condition (encoding plus comparison/decision) performance, M.L. shows alpha power reductions (i.e., levels of activation) that are generally smaller than those shown by neurologically intact individuals, an overall decline in activity not unexpected given the extent of her injury. Moreover, her LH is more active than her RH during encoding and comparison/decision processes, a pattern that is quite different from the normal participants studied in Experiment 1 where significant right frontal lobe activation was obtained. Curiously, M.L. inhibits the right frontal area during such processing.

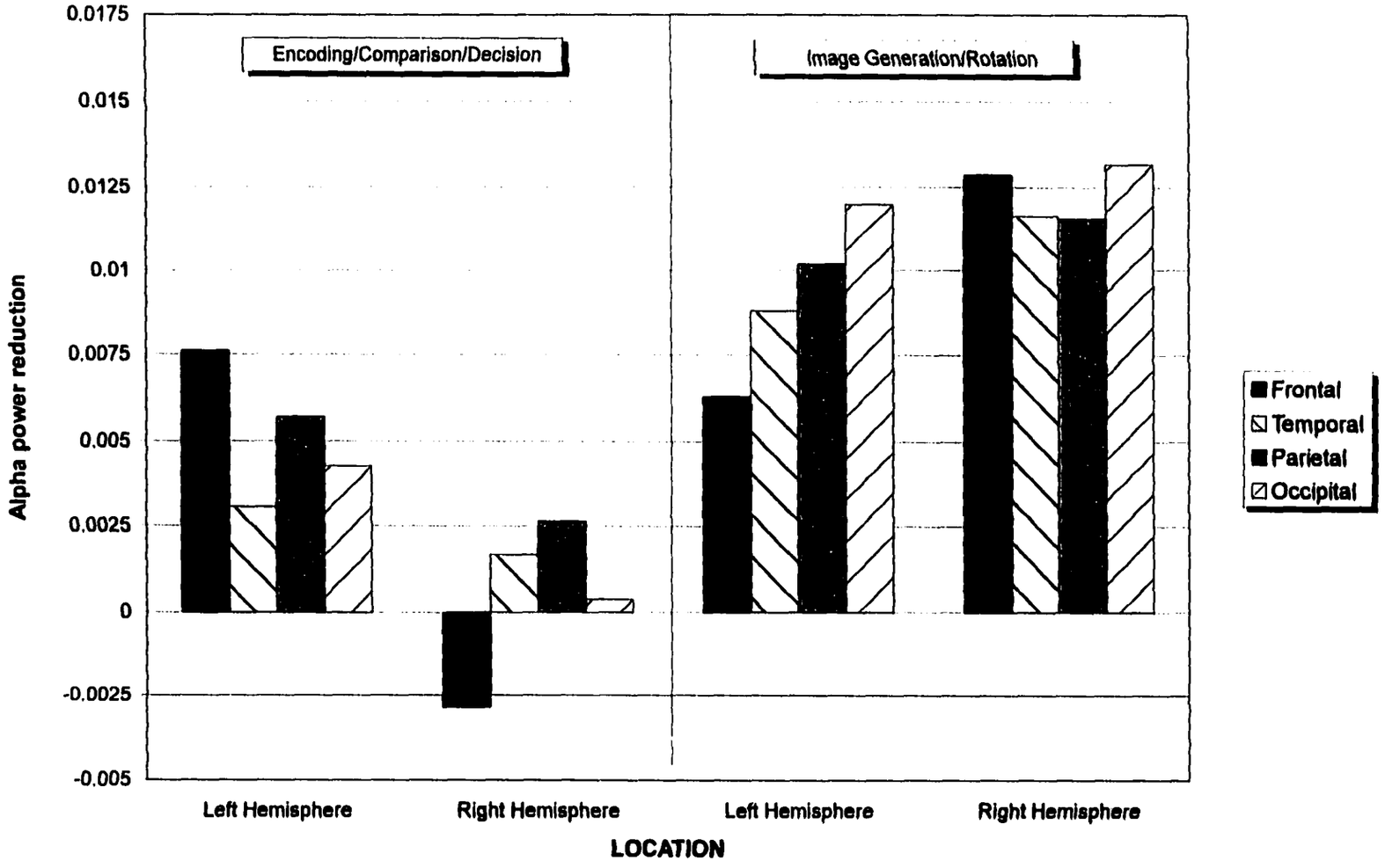


Figure 7: Alpha Power Reductions (V^2/Hz) for Encoding/Comparison/Decision and Image Generation/Rotation in Patient M.L.

In the Rotate condition (image generation and rotation), M.L. produces a pattern of activation that is directly opposite of that found in the neurologically intact individuals of Experiment 1: she shows enhanced activation of the RH in contrast to their predominantly LH activation. Again, this shift in brain locale is not unexpected in light of the significant damage to her left temporal lobe with apparent compensatory increases in activation in the right hemisphere parietal and temporal regions. This altered pattern of activation may be related to the ineffectual mental rotation performance that patient M.L. exhibits.

INVESTIGATION OF INTERNAL IMAGE GENERATION USING THE HOLTZMAN INKBLOTS TECHNIQUE

To further investigate the brain areas mediating complex image generation, a novel task situation, namely the Holtzman Inkblot Technique (HIT) (Holtzman, 1968) (see Figure 8) was employed. Although a mainstay in the field of assessment of psychological disorders, HIT has rarely been used in the field of experimental cognitive psychology.

Experiment 3

Stimulus Materials

The intent of the HIT was to create "a new inkblot technique, having ratings of demonstrated psychometric value, while preserving the qualitative characteristics of the Rorschach" (Holtzman, Thorpe, Swartz and Herron, 1961). The fact that HIT not only claims, but is apparently psychometrically superior to the Rorschach technique (e.g., better inter and intra-scorer reliability), leads Gamble (1972) to suggest that it might eventually replace the Rorschach technique as its natural successor.

The HIT consists of two tests containing 45 inkblots. It is important, for the purposes of present study, that in the selection of a given blot an important consideration was the ability to "elicit small detail, space, color, and shading determined responses from the subject" (Gamble, 1972). This characteristic of the HIT suggests that generated images are very vivid and detailed internal representations of the verbally reported interpretations. One additional characteristic of the HIT differing from that of the Rorschach is the requirement that the participant give only one response to each card as compared to an open ended response.

Figure 8: An example of a Holtzman Inkblot

This provision further enhances the psychometric properties of HIT (Gamble, 1972) as codification of a singular response as compared to scoring an open ended, potentially very long, multiple responses is more consistent.

The criteria for inclusion of a given blot into the original HIT set were;

1. the ability to discriminate between college students and hospitalized psychotics
2. the amount that a blot contributed to a rating on several variables (e.g., location, color, shading, movement)
3. inter- and intra-rater reliability

The following are the 22 variables on which participants receive a rating for the HIT (Holtzman, 1968);

- Reaction time - time from presentation of inkblot to the beginning of the primary response
- Rejection - when participant returns the card without response (rating 1)
- Location - tendency to break down the inkblot into smaller regions (rating 0 for entire inkblot, 1 for use of a large area of the blot, and 2 for use of smaller areas of the blot.
- Space - rating 1 for figure-ground reversal involving responses.
- Form definiteness - 5 point scale ranging from 0 for indefinite forms (pile of smashed pumpkins) to 5 for highly defined forms (man on a horse)
- Form appropriateness - how well does the response concept match the form of the inkblot (0-poor, 1-fair, 2-good)
- Color - rating of importance of color (both chromatic and achromatic) as a response determinant. Rating equals 0 when color information no used, 1 when used in secondary manner, 2 when color is a primary factor in the response which also includes or implies some indefinite form, 3 when color is primary and no form is present.
- Shading - rating of importance of shading or texture in the response. Rating 0 when not used, 1 when used only in a secondary manner and 2 when shading is a primary determinant.

- Movement - a five point scale for measuring the degree of movement, tension, or dynamic energy as perceived by the participant regardless of the content. Rating 0 for none, 1 for static potential (sitting, looking, etc.), 2 for casual movement (walking, talking), 3 for dynamic movement (dancing, weeping), and 4 for violent movement (exploding).
- Pathognomic verbalization - a five point scale ranging from 0 (i.e., no pathology present) to 4 (very bizarre verbalizations). The intent is to assess the degree of disordered thinking (i.e., fabulizations, fabulized combinations, queer responses, incoherence, autistic logisms, contaminations, self-references, absurd responses, etc.)
- Integration - a measure of success in integrating elements of a blot into a larger whole. Rating 1 when two or more elements organized into a larger whole.
- Human - rating 0 when no human content is included in the response, 1 for human parts, featureless wholes and cartoon characters, 2 for identifiable humans or the human faces elaborated.
- Animal - similar to Human, rating 0 for no animal content, 1 for animal parts and 2 for whole animals
- Anatomy - rating 0 for no penetration of the body wall, 1 for X-rays, medical drawings, and bone structures, and finally 2 for visceral organs.
- Sex - rating 0 when no direct sexual references are made, 1 for socially acceptable sexual activities and expressions (e.g., kissing) in the subjects report, and 2 for explicitly sexual references (e.g., penis)

- Abstract - measuring the amount of abstract content in subjects report. Rating 0 if no abstract content is present, 1 if abstract elements are of secondary importance in the report, and 2 if the entire response is abstract in nature (e.g., happiness)
- Anxiety - is a three point measuring scale for the amount of anxiety content in the participant's response. Anxiety may be reflected as reflected in feelings and attitudes (e.g., frightened), expressive behavior (e.g., escaping), symbolic responses (e.g., dead), or culturally determined symbols of fear (e.g., murderer). Rating 0 when absent, 1 when the content is debatable, and 2 when the presence of anxiety is clearly apparent.
- Hostility - 4 point measuring the amount of hostility apparent in the content with increasing rating as hostility increases from vague to direct, violent expressions in which human beings are involved.
- Barrier - rating of 1 if there is any reference protective covering of any sort (e.g., membrane, shell, etc.) in the subjects response
- Penetration - rating 1 for concepts symbolizing any type of body penetration
- Balance - rating 1 when subjects are expressing concerns over asymmetry/symmetry of inkblot itself
- Popular - rating 1 if popular (predefined most frequent responses for specific areas of inkblot as determined by the normative studies of HIT) response is given (Gamble, 1972)

When tested for their ability to differentiate a college student from a hospitalized psychotic it was found that, remarkably similarly to the Rorschach, ratings for location, form

appropriateness, form definiteness, movement and shading were all higher in college group. Interestingly, there was no difference in ratings for color, but greater variance was noted among psychotics (Holtzman, Thorpe, Swartz, and Herron, 1961). In fact, Leichsering (1993), using the 30 card version of HIT, was able to appropriately differentiate not only chronic schizophrenics from acute schizophrenics and borderline patients, but also borderline patients from neurotics.

The intent behind the choice of the HIT as a test for investigating the brain regions activated during mental imagery is the based on the following set of assumptions. First, when one perceives an object or situation that is actually (physically) present, our current understanding of the visual system suggests that this visual percept is analyzed, and an internal representation is generated. The image is subsequently positioned in a coordinate space system and a match is found among various images stored in the participant's memory. This memory match may be used as a template for the reporting of the objects identity or its situational properties.

When a participant is presented with an inkblot from the HIT set, there is no "real" object or situation contained in such a representation, and thus, there is no direct memory match. Rather, a variety of memory locations or cell assemblies are likely to be stimulated in search of the most salient/reasonable match for the internal representation of the given inkblot. As this search through memory is performed, a variety of internal images are "tried" as matches, and ultimately one (the closest match) is chosen. Obviously, neither the object match, nor that which is actually perceived within the inkblot, are physically represented in

the visual reality of the inkblot stimulus. Therefore, one infers that what a given participant reports is an internally generated and named image of something that is not really there but has its origin in some memory trace.

It is this process of internal generation of a complex image that is of primary interest to Experiment 3. To be able to determine which areas of the brain are selectively engaged during HIT image generation, two additional control conditions, independent of the brain activity induced during HIT performance, were developed. One control condition consists of 12 slides containing simple drawings of objects which are easily recognizable by college students (e.g., wrist watch)(see Figure 9).

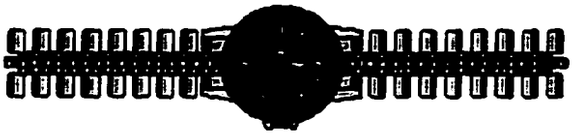


Figure 9: An example of a simple object test stimulus

This condition should produce increased activity in regions of the brain which are responsible, or play a role in simple object perception, but not necessarily complex image generation as in the HIT.

The second control condition consists of 12 slides containing simple drawings of situations (e.g., a physical examination, handshake, typing, computing, filing, etc.)(see Figure 10).

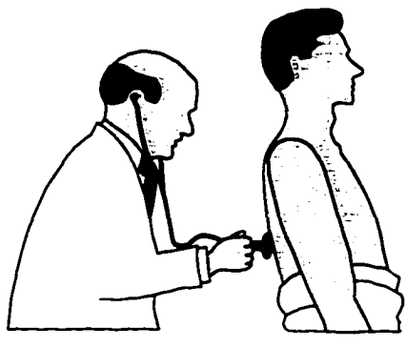


Figure 10: An example of a simple situation stimulus

These latter drawings were designed to elicit increased activation in brain regions subserving not only object identification, but also identification of objects in complex relationships to one another. This condition was employed because inkblots are sometimes reported by participants as being objects in motion or in some dynamic relationship to other "forms" depicted in the visual display.

The difference in activation levels from baseline (a blank slide) to object recognition (OR), to the situation recognition (SR) stimulus, when contrasted with HIT, could reveal the areas of the brain that are most prominently involved in complex image generation. Information from Experiment 3 should supplement the findings from Experiments 1 and 2 in that the right frontal and left parietal lobes are expected to be particularly involved in this process as also suggested by research on brain damaged individuals.

Additionally, in a fourth experiment, an attempt to further explore the role of the frontal lobes in complex image generation will be conducted. An individual suffering from

schizophrenia will be used as a participant, as schizophrenics are known to exhibit poor performance on the HIT as compared to normal individuals (i.e., reporting static potential rather than dynamic movements, a greater degree of image integration, and less color information (Holtzman, Thorpe, Swartz, and Herron, 1961; Leichsering 1993). Additionally, schizophrenics are known to exhibit relative hypoactivation of the frontal lobes while performing complex cognitive tasks like Wisconsin Card Sorting (Weinberger, Berman, Zec, and Weinberger, 1986; Berman et. al., 1986; Buchsbaum and Haier, 1987). The combination of the above two factors might shed additional light on the contribution of the frontal lobes to the performance of complex image generation. Namely, if the frontal lobes are involved in preplanning organized behavior, their dysfunction in schizophrenic patients should significantly inhibit performance on the HIT. The logic here is that to be able to perform the HIT task, in addition to encoding the visually perceived inkblot, a series of internally generated (from memory) images must be matched to the inkblot, and preserved frontal lobe function should be necessary for appropriate initiation and sequencing of these processes. Thus, as Luria (1973) stated, it is "the ability to create *stable motives* of recall and to maintain the *active effort* required for voluntary recall, on the one hand, and the ability to *switch from one group of traces to another*, with the result that it is the process of recall and reproduction of material which is significantly impaired" in patients with lesions to frontal lobes. Resultingly, these patients often report and interpret the very first feature that they perceive without consideration of the gestalt and the remainder of the stimulus presented, and thus produce erroneous responses (Luria, 1973).

Participants and Procedure

Fourteen right-handed male undergraduates at Iowa State University (aged 18-22 years) participated in the Experiment 3. Right hand preference was determined by using a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). Prior to the experiment, participants read a set of instructions and were shown an example inkblot (which was not part of the experimental set). The experimenter then instructed the participants on how to react and to respond to each of these conditions (i.e., OR, SR and HIT). Participants were seated in a reclining chair in an electrically shielded and sound attenuated chamber.

Design

During the experiment, all participants received four blocks of trials (Baseline, OR, SR and HIT). Baseline trials consisted of 5 blank slides with a 5 sec recording epoch; The OR and SR conditions consisted of 12 slides each, with a 5 sec recording epoch; the HIT condition was comprised of 12 slides with a 40 sec epoch. Baseline slides were always presented first and were followed by the three blocks of task conditions counterbalanced in a Latin Square. All stimuli were presented on a 15" VGA computer monitor (256 color resolution) at a viewing distance of 1.5m. After the recording interval, subjects were asked to verbally describe the most striking and prominent image they were able to "see" in the inkblot. This response was recorded by the experimenter. The same procedure was followed in the OR and SR conditions. In the OR and the SR conditions, EEG recordings were initiated by the experimenter, and after 5 seconds, participants were asked to describe the object/situation they thought was depicted in the slide presented.

As in the first two experiments, an eight channel Grass electroencephalograph and an ECI electrode cap (Blom and Anneveldt, 1982) were used to monitor alpha activity at sites Fp1, Fp2, T3, T4, P3, P4, O1 and O2 (Jasper, 1958). Linked earlobes (A1 + A2) served as reference leads and electrode impedance was maintained below 10kΩ. The eight channels were calibrated to a standard of 50μV and EEG was digitized on-line by microcomputer at 100 samples per sec using Unkelscope® data acquisition software. Eye blinks were edited from the recording, and alpha waves isolated using an 8-12 Hz bandpass filter. Power spectral analyses were performed on the resulting 328 [(2 hemisphere x 4 location) x (5 baseline + 12 OR + 12 SR + 12 HIT) filtered recordings.

Results and Discussion

A 2(hemisphere) x 4(location) x 3(task) repeated measures ANOVA revealed that, while overall activation of hemispheres was not significantly different, specific regions of brain did differ in their activation level [$F(3,104)=4.53$, $p<0.005$] (see Figure 11). Specifically, a Tukey's HSD post-hoc test revealed that the occipital and parietal lobes were more active in performance of all tasks than were the frontal and/or the temporal regions, but were not different from one another. Moreover, different tasks produced differing levels of brain activation [$F(2,208)=204.48$, $p<0.0001$], with HIT producing the greatest amount of brain activation, followed by SR and lastly OR which did not differ from one another. A significant interaction of Location x Task was also revealed [$F(6,208)=3.03$, $p<0.008$] as well as marginally significant three way Hemisphere x Location x Task interaction [$F(6,208)=1.98$, $p=0.06$].

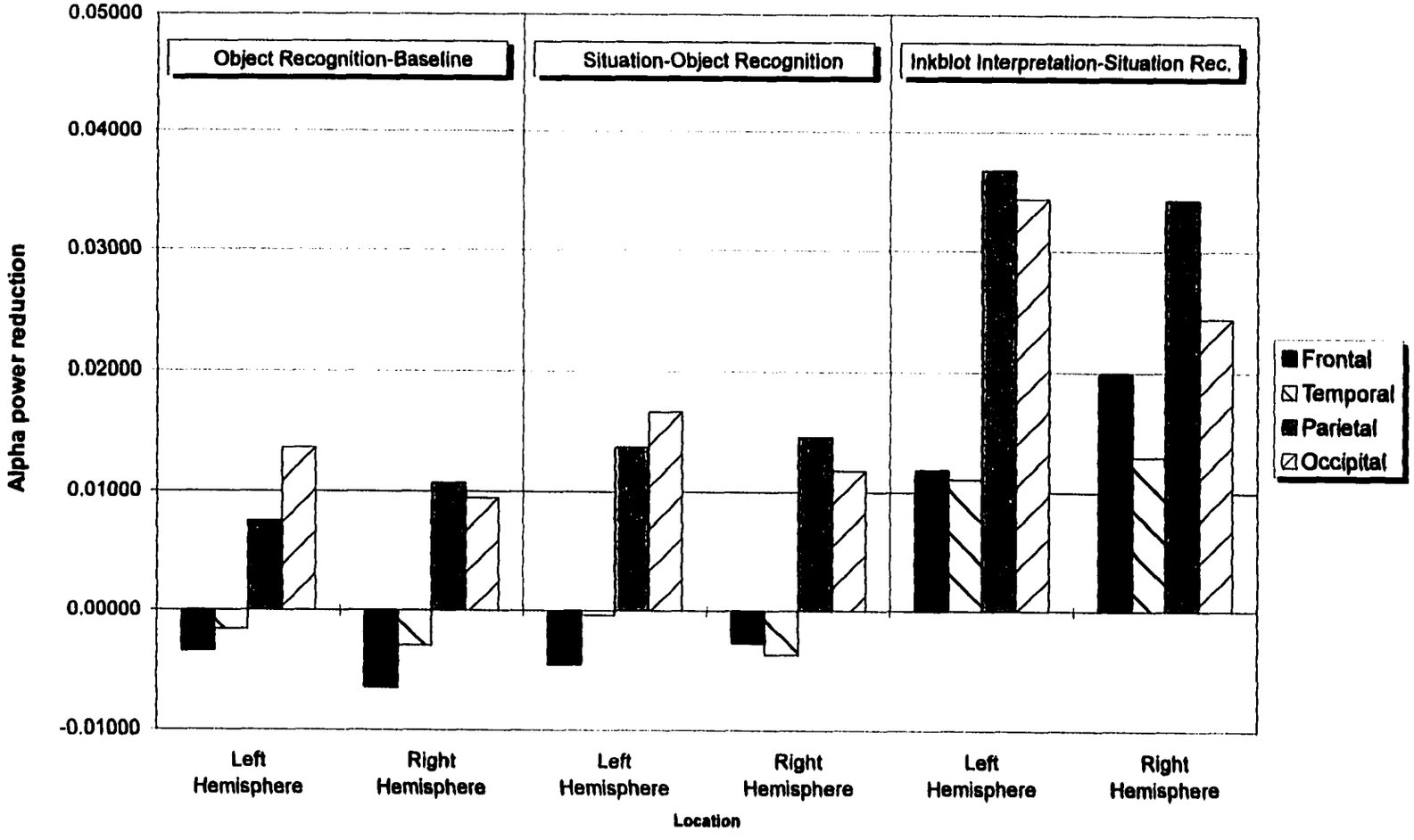


Figure 11: Alpha Power Reductions (V^2/Hz) for Object Recognition, Situation Recognition and Inkblot Interpretation Tasks in Neurologically Normal Individuals

To further investigate the sources of these interactions, post-hoc Tukey's HSD test revealed that for OR and SR there was no left-right asymmetry in brain activation patterns, but there was a clear difference in the anterior-posterior direction, with the occipital and parietal lobes being significantly more active during the performance of all three conditions than frontal and temporal locations ($p<0.05$).

The activational pattern for inkblot interpretation task was somewhat different. As revealed by post-hoc analysis, while the aforementioned anterior-posterior distribution was preserved, there was also a significantly increased level of involvement of the right frontal region (which is now significantly more active than the left frontal lobe), and a somewhat lesser involvement of the right occipital region, which is now less active than both the left parietal and left occipital region; i.e., it maintains an activation level close to that of the right parietal lobe.

This pattern matches the proposed brain mapping of the functional system subserving image generation and mental rotation processes as hypothesized in Experiments 1 and 2. Namely, the occipital and parietal lobes subserve the encoding of a visual image. The fact that in Experiment 1 there was enhanced activation of the left parietal lobe during the performance of the MRT, indicates that this region was preferentially activated when processing stimuli that require the construction and buffering of three-dimensional internal representations. In the Experiment 3, due to a variety of stimuli encompassing animate and inanimate objects and the virtually limitless possibilities of an inkblot, it is likely that both the left and the right parietal lobe activity is required for task performance (see Figure 12).

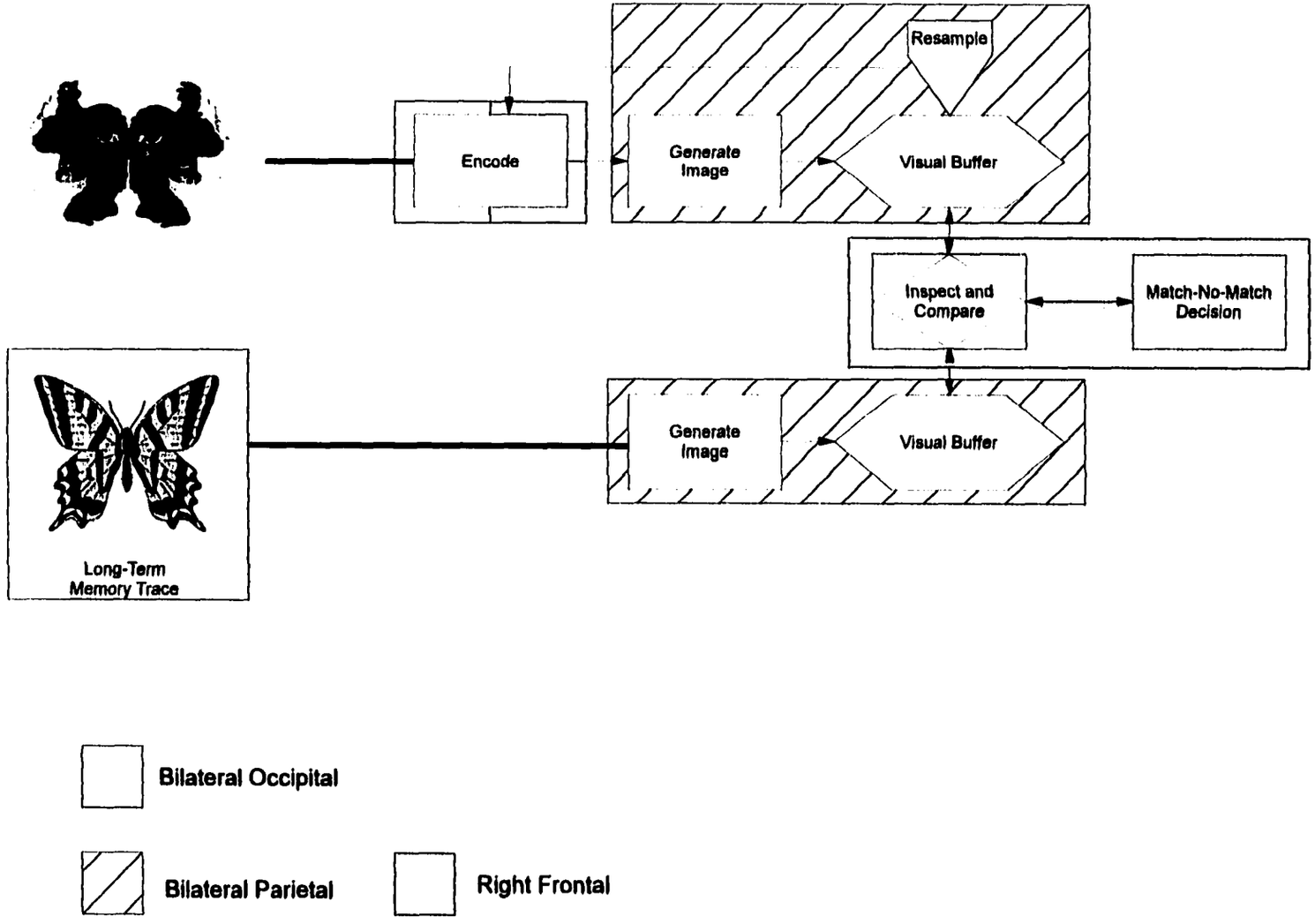


Figure 12: Model of Subcomponent Processes Comprising Mental Image Generation

Of particular importance, however, is the absence of left temporal lobe activation during any of the task conditions of Experiment 3. As the results of Experiments 1 and 2 suggested, the function of the left temporal lobe is the mediation of the mental rotation process separate from image generation. In OR, SR and HIT no mental rotation was necessary, and thus the activation of all regions associated with image generation as found in Experiments 1 and 2, except the left temporal lobe was obtained. This provides converging evidence that the left temporal lobe does not obviously participate in visual image generation, which appears to be the purview of the parietal cortices, but it does selectively mediate the process of mental rotation.

Experiment 4 (A Case Study)

The prominent role played by the frontal lobes in the HIT was anticipated, due to their known role as organizers and planners of purposeful mental activity (Luria, 1973). And, given that schizophrenic patients' performance of the HIT produces lower ratings as compared to normals, it seems possible that this impoverished performance may be related to a relative failure of frontal lobe functioning in such patients (Andreasen, 1989).

To further investigate the role of the frontal lobe in image generation, a patient suffering from schizophrenia was recruited from a local treatment facility. This individual was studied in an effort to determine whether there is a discernible relationship between the low image generation performance as measured by the HIT and the frontal lobe dysfunction as recorded by the EEG.

Behaviorally, unmedicated schizophrenics are unable to maintain contextual information and utilize it to inhibit inappropriate responses. (Servan-Schreiber, Cohen and

Steingard, 1996). Physiologically, as will be discussed below, schizophrenic patients have been found to show lesser activation of the frontal regions than normal individuals both at rest and during cognitive engagement (Andreasen, 1989; Weinberger, Berman and Zec, 1986). If indeed the frontal cortex is involved in planning tasks and the organizing of complex mental activity (like the processes involved in Experiment 3) one can envision how the internal generation of HIT images, and locating a best memory match for a given inkblot, could be impaired in such patients.

Given that Experiment 4 is exploratory in nature and is based on a theory of pathophysiology underlying schizophrenia that is still not unanimously accepted, there is a need to provide some background for the rationale behind involvement of this special population. To that end, the following pages are devoted to a selective discussion of the relevant research on the structural and functional abnormalities of the schizophrenic brain. For a more exhaustive discussion of etiology of schizophrenia see Willson, O'Leary and Nathan (1992).

Symptomatology of Schizophrenia

Schizophrenia generally involves impairment in several areas of functioning and presents itself with multiple symptoms. Serious disturbances of thought (delusions), and perception (hallucinations), or certain disturbances of affect must be present for accurate diagnosis.

The following are the common symptoms manifest in schizophrenia;

Thought disorders:

1.) Disorders of form and process (language and communication disorders)

2.) Disorders of content (confused ideas)

Perception Disturbances:

3.) Hallucinations

Affect Disturbances:

4.) Blunt affect

5.) Inappropriate affect

Psychomotor Disturbances:

6.) Mannerisms, posturing, and grimacing

7.) Catalepsy

8.) Tardive dyskinesia

Positive and Negative Symptoms in Schizophrenia

There are an increasing number of researchers who believe that an alternative classification of schizophrenia symptomatology into positive and negative symptoms could be more useful and informative than current DSM-III-R (1987) classification because it can be more easily related to neurological (e.g., neurotransmitter) systems. This classification is also the one which incorporates the hypothetical dysfunction of the frontal lobes in such patients.

Positive symptoms are the "excess" symptoms such as hallucinations, delusions and other thought disorder related symptoms, while negative symptoms encompass such "deficits" as flat affect, lack of drive and relative absence of speech. It has been empirically determined that positive symptoms respond better to the pharmacological therapy than

negative ones. The relevance of the underlying biology of positive and negative symptoms for the image generation and mental rotation are discussed below.

Andreasen (1989) has developed a convincing theory to account for the neural substrate of both positive and negative symptomatology in schizophrenia. As previously mentioned, in the simplest of terms, negative symptoms represent a loss or decrease in normal functions, while positive symptoms result from distortions or excess of normal functions. Looking at the character of the symptomatology provides some insights as to the biological origins of the disease.

For example, negative symptoms such as alogia (i.e., loss of fluency of thought and speech), affective blunting, avolition, anhedonia (i.e., loss of hedonic capacity) and attentional impairment (i.e., inability to direct and maintain attention) are thought to be mediated by the frontal lobes (Goldman-Rakic, 1987; Stuss and Benson, 1986, 1987). It is therefore logical to consider the impaired functioning of the frontal lobes when investigating the neurological origins of negative symptoms in schizophrenia.

Positive symptomatology has proved to be somewhat more difficult to explain. If hallucinations are of an auditory type, one might consider abnormal neuronal circuitry in the auditory cortex, the temporal association cortex, or memories in the temporo-limbic regions such as the amygdala or hippocampus as their cause. Delusions, disorganized speech, and grossly disturbed judgment are all difficult if not impossible to localize at our current level of knowledge of brain function.

Structural/Anatomical Abnormalities of the Brain in Schizophrenia

One of the first structural anomalies of the schizophrenic brain described was the abnormality in ventricle size (upon post mortem brain analysis). This was later confirmed through the use of CT, when it became possible to observe anatomical changes in living patients in different stages of the illness. MRI was yet another improvement on brain imaging techniques with the significant enhancement of image resolution providing greater detail. The findings of studies utilizing MRI have confirmed the previously discussed findings of CAT scan studies (Andreasen, Nasrallah and Dunn, 1986)

The finding of enlarged ventricles in schizophrenic patients suggests that this enlargement is a consequence of the compensatory process that replaces the "disappearing" periventricular tissue (Pfefferbaum, Lim, Rosenbloom and Zipurski, 1990). As structures in the periventricular regions of the brain are known to have important cognitive and motor functions, damage to this region could conceivably have behavioral consequences that would resemble schizophrenia. The theory that some damage occurs in the periventricular regions is, however, not fully supported by pathological findings. It appears that, although some neural loss in the limbic structures occurs, it is not followed by complementary evidence of gliosis (i.e., proliferation of glia).

An additional brain structural abnormality reported in studies of schizophrenia is that of atrophy of the frontal lobes. This atrophy is apparently more pronounced on the left side (the meaning of this asymmetry is still unclear) (see Seidman, 1983), and is greater for patients with predominantly negative symptomatology than for those with positive symptomatology (Andreasen, 1988).

More recent studies have revealed structural changes that encompass neuronal loss and disturbances in neuronal distribution which are apparently localized to the frontal and temporal lobes, and have also been found in limbic structures such as the hippocampus and amygdala. These findings, again, require additional confirmation to determine that they are indeed characteristics of the schizophrenic brain (Roberts, 1991).

Investigation of the stage of disease and its relationship with cortical gray matter volume has also revealed that relative cortical gray matter deficit and lateral ventricle enlargement are present as early as 6 months from the onset of illness. Given its presence so early in development, this finding suggests that there are preexisting structural brain deficits precipitating the onset of schizophrenia (Lim, Tew, Kushnr, Chow, Matsumoto and DeLisi, 1996).

Functional Abnormalities of the Brain in Schizophrenia

Several recent technological advances provide research on the workings of living brains with several very powerful techniques (e.g., PET and fMRI). In particular, they have been extensively used to investigate whether or not the activation of the brain of a schizophrenic patient differs in profile from a "normal" brain. The findings of abnormally low levels of activity in the frontal regions (hypofrontality) generally supports the notion of decreased function of frontal lobes in schizophrenia. This finding, however, has not always been replicated.

Other recent studies have attempted to measure cerebral blood flow during performance of cognitive tasks known to be mediated by the frontal lobes (e.g., during the Wisconsin Card Sorting test) (Weinberger, Berman and Zec, 1986; Berman, Zec and

Weinberger, 1986; Buchsbaum and Haier, 1987). Such studies conducted on schizophrenic individuals have revealed that these patients have difficulties in activating their frontal lobes for the purpose of accomplishing various cognitive tasks. Complementary findings of PET studies (Gur et al., 1987) on the relative increase in metabolic activity in the basal ganglia, coupled with this finding of hypofrontality, suggests that Andreasen's account concerning the mixture of positive and negative symptoms in schizophrenia, is indeed viable.

Still other studies have demonstrated how activity of the frontal lobes is necessary for the successful organization of purposeful behavior, and how functionally and anatomically interconnected the frontal lobes are to other regions of the brain. Bannon and Roth (1983) in their animal studies, found that selective damage to the dopaminergic neurotransmitter system of the frontal lobes produces an increase in dopaminergic activity in various subcortical regions, most notably the basal ganglia. If indeed there is an increase in the number of D2 receptors in the basal ganglia (Seeman, Niznik, and Guan, 1990; Seeman, Ulpian, Bergeron, et al., 1984), and if these mediate the subcortical hyperactivity, it should be possible to detect this hyperactivation in vivo via PET scanning. Unfortunately, such attempts have produced inconclusive results (Andreasen, 1989).

The Bannon and Roth (1983) finding is interesting in that it might explain why patients with schizophrenia can simultaneously exhibit positive and negative symptoms and it further offers support for the theory in which the hypofrontal activity might express itself as the negative symptoms of schizophrenia, while hyperdopaminergic activity in the basal ganglia might be manifest as abnormalities in movement and other positive symptoms such as hallucinations. These two phenomenological clusters would be interrelated through

dopaminergic activity of the frontal lobes which may lead to hyperactivity of subcortical regions.

Targeting of the dopaminergic system as partially responsible for the etiology of schizophrenia stems from the fact that, despite our lack of knowledge about the origins of this disease, it has been empirically shown that delusions and hallucinations (required for the diagnosis of schizophrenia) generally respond to such antipsychotic drugs as haloperidol, chlorpromazine, remoxipiride, risperidone, and clozapine. As the mechanism of action of these drugs is the blockade of D2 receptors in vivo (Anden et al., 1970) and in vitro (Seeman et al., 1975)(except Clozapine which acts through D4 receptors), the idea is that at least part of schizophrenic symptomatology is dopamine mediated (Seeman, 1987; Seeman, 1993; Seeman, Bzowej, Guan, Bergeron, Reynolds, Bird, Riederer, Jellinger and Tourtellotte, 1987). A finding lending support to this hypothesis is that dopaminergic activity increasing drugs (e.g., amphetamines) may trigger psychotic symptomatology similar to that of paranoid schizophrenia in otherwise psychoneurologically normal individuals (Sunahara, Seeman, Van Tol and Niznik, 1993).

The relatively recent work of Williams and Goldman-Rakic (1995), using iontophoresis of drugs in prefrontal cortex of the monkey brain, have suggested an even more important role of dopamine in behavior regulation. Namely, the process of holding stimuli on-line for an extended period of time while a response strategy is being planned is apparently disrupted with the introduction of a D1 blocker. In their study, a spatial delay response task was conducted. In this procedure, a monkey was trained to remember a location of a cue flashed to a screen and to make an eye movement to that position after a

short delay. During task performance, the firing of cells in the frontal lobes was monitored through implanted electrodes. A number of cells became active during this task and continued their activity during the delay part of the task (i.e., the period in which the location of the cue had to be maintained on-line). In fact, this cellular activity was registered only when the cue was positioned in that particular section of the visual field (the 'memory field'). When a D1 blocker was applied using iontophoresis, activity due to the delay was enhanced, but only for those stimuli that fell within the cell's memory field. As Desimone (1995) argues, this was a surprising result in light of previous findings on the impairment of working memory due to injections of D1 antagonists (Arnsten, Cai, Murphy and Goldman-Rakic, 1994). However, at the higher injection iontophoretic currents, even in the Williams and Goldman Rakic study, a general inhibition of cell firing was noted. Such nonspecific inhibition mimicked that of injecting any amount of D2 antagonists. Desimone (1995) further argues that these cells are sensitive to both the number of receptors occupied by the transmitter, as well as to the specific dopamine receptor contacted.

In summary, the above anatomical/physiological findings complement each other in a logical manner, and serve as the basis for a very plausible theory of genesis and development of schizophrenia. One can envision the disorder beginning with a slight dysfunction of the frontal lobes (due to some structural or functional abnormality). At first, this is insufficient to produce any negative symptomatology as sufficient frontal lobe function is still preserved. However, since the subcortical structures are under retrograde control from cortical regions, and especially from the frontal lobes, one might expect uncontrolled hyperactivity of subcortical regions, more specifically the basal ganglia and thalamus, due to the failing of the

frontal lobes to downregulate their functioning. This subcortical hyperactivity would then give rise to positive symptoms which are prominent in the clinical picture until the frontal lobes deteriorate to the point where negative symptoms eventually appear. Finally, in the end, one would see a predominance of the negative symptoms (i.e., increase in the dysfunction of the frontal regions) with the autodownregulation of subcortical regions due to cell exhaustion. This stage of the disease is frequently called "burned out schizophrenia" suggesting the complete dysfunction of the basal ganglia, with only some remnants of positive symptoms (Andreasen, 1989).

As Experiments 1, 2 and 3 have suggested that the activation of the right frontal lobe is required for performance of the given tasks, and strong indications for localization of the mental rotation and mental image generation processes, there was a need to better isolate the planning and execution of these subcomponents which are theoretically linked to the frontal lobes. A schizophrenic individual should, due to the relative impairment of the frontal lobe function, have difficulties in performing a complex image generation task like the HIT. Successful performance here requires preplanned and organized behavior in which a series of memory based visual images are activated and compared to the presented inkblot. Subsequently, a verbal response is made (the latter being another frontal lobe function). It is expected that the brain activation pattern of schizophrenic individual should match that of normal individuals with the exception that the frontal lobes should be less active. Consequently, the schizophrenic patient's performance of the HIT task should also be lower from that of normal individuals as previously shown (Leichsering, 1991).

Participant

Patient D.K. was diagnosed as suffering from schizophrenia in 1961. His participation was voluntary and he was remunerated $10.00 for his efforts. D.K. was selected from a pool of patients asked by local treatment providers to participate in this study. The selection criterion was that the patient be a moderately functioning individual who is compliant with his/her therapeutic regimen and would be able to participate in tasks such as the HIT.

Materials and Procedure

The experimental materials and procedure were identical to those described in Experiment 3, as was the instrumentation and electrophysiological methodology.

Design

The design matched that described in Experiment 3.

Results and Discussion

Patient D.K.'s verbal responses to each of the HIT stimuli can be found in Table 1. His performance of this task revealed slightly poorer responses to inkblots initially. But, as the HIT task progressed, D.K.'s responses became increasingly richer in content (as can be seen in Table 1) and thus qualitatively closer to the responses of normal individuals.

Electroencephalographic recordings during the performance of the HIT revealed a different activation pattern from that found in neurologically normal individuals (see Figure 13). In general, patient D.K. exhibited less activation in each of the three experimental conditions. More specifically, in the OR and SR conditions none of the brain regions monitored by EEG demonstrated any significant activation relative to baseline. It should be

mentioned that, aside from two objects, all other OR and SR stimulus items were appropriately recognized (91.7% accurate). As found in Experiment 3, neurologically normal individuals had a pronounced activation of both the left and right occipital and parietal regions while D.K. did not.

Of particular interest was that the activational pattern for the HIT condition elicited by D.K. (Figure 13) which shows significantly more activity than either in the OR or SR conditions. This activation was particularly pronounced over the left and right parietal regions, and even more so over the right frontal cortex. There was a notable asymmetry between the activation of the right frontal lobe as compared to the left frontal lobe

Table 1: D.K.'s HIT responses

Inkblot	D.K.'s response
1	Two guys looking at one another examining something in the center
2	Two guys at the top hanging down
3	Two people on the outer edges around a tree trunk
4	Two roosters looking at one another (top part)
5	Two people looking at one another wearing head ornaments
6	Two maids getting ready to stir something with prongs
7	Two feet with shoes at the bottom (trousers hanging over)
8	Two guys dancing around chandelier
9	Two hens sitting on top of two geese
10	Butterfly trying to land on hot coals
11	Two hourglasses side by side, guy at the center waiting for them
12	Two women looking at each other celebrating something on the floor

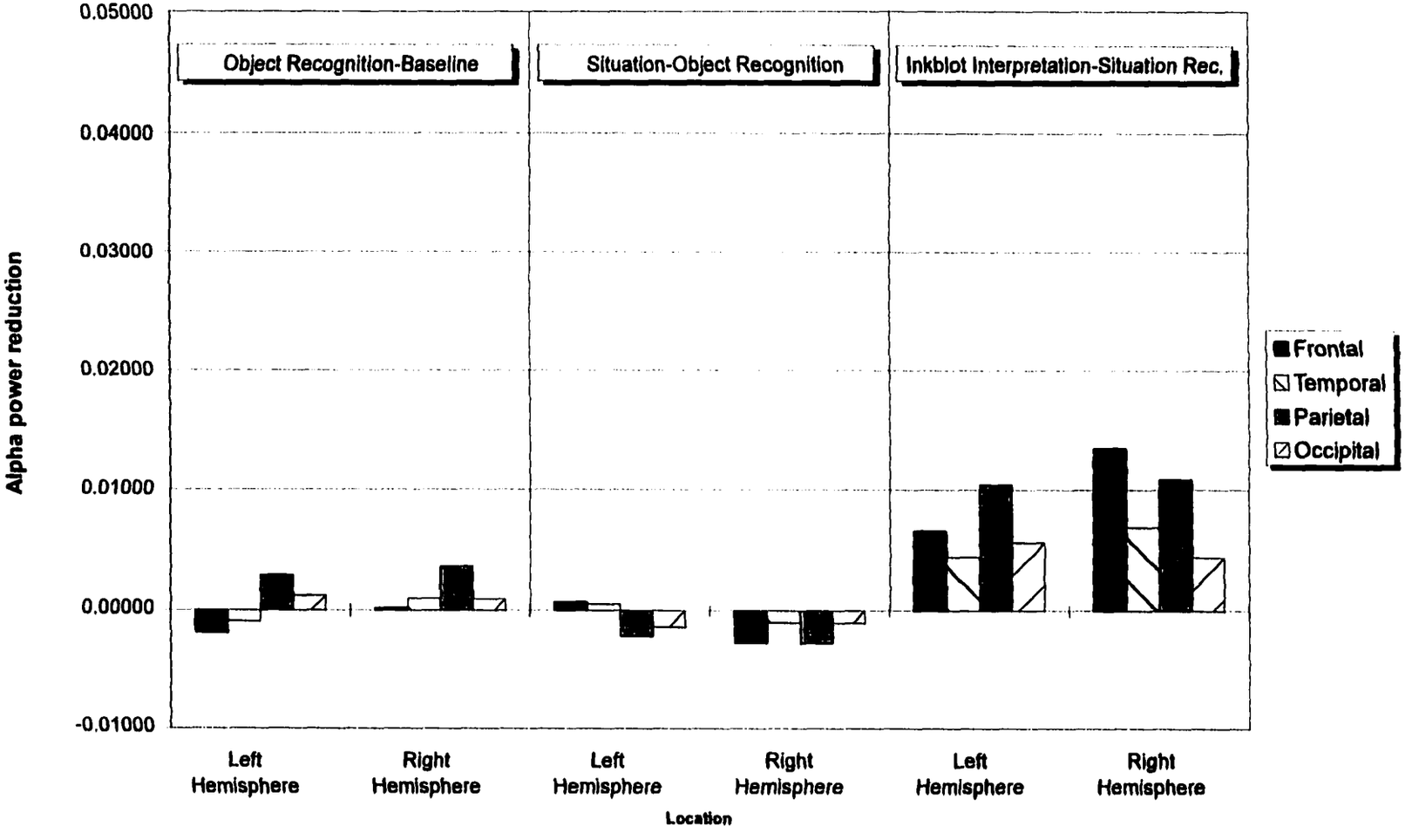


Figure 13: Alpha Power Reductions (V^2/Hz) for Object Recognition, Situation Recognition and Inkblot Interpretation Tasks in Patient D.K.

(favoring the right) that is consistent with the pattern of frontal lobe activation in all previous experiments involving normal participants.

The activational pattern exhibited by D.K. suggests that he was able to engage right frontal lobe resources to perform the HIT, a pattern that provides a possible explanation for why D.K.'s responses to the HIT were more "normal" than would otherwise be expected.

GENERAL DISCUSSION

The intent of the experiments conducted in this dissertation was to highlight the cooperative manner in which multiple brain regions interact in order to perform complex mental tasks, in this case, mental image generation and mental rotation. The results of Experiments 1 and 2 provided a preliminary mapping of the cortical areas selectively engaged during each subcomponent process of the mental rotation process. This mapping is superimposed on Figure 3. Additionally, these results indicated that there is a functional system in evidence, comprised of several brain locations that actively participate in the performance of such a task.

As previously discussed, the model of the functional system subserving the processes of mental image generation and rotation posits that initial encoding of the visual inputs is handled bilaterally via primary visual cortex (Hubel and Wiesel, 1979; Zeki, 1993; Van Essen, Anderson and Felleman, 1992) under the auspices of the right frontal lobe. The frontal lobes are not only involved in guidance of the visual system (Goldman-Rakic, 1987), but also coordinate latter subcomponents involved in performance of this task (Luria, 1983). The neural representations generated by the visual cortex are then likely shunted to the left parietal lobe which mediates the internal generation and maintenance of the more complex 3-D images necessary for successful mental rotation (Goldenberg, 1992).

As parietal lobe function is necessary for maintaining information about directionality, as well as the creation of three dimensional representations, it also most likely serves as the locus of the visual buffer as illustrated in Figures 12 and 14 (Critchley, 1971; Butters and Barton, 1970). That the left parietal area was most active during the Rotate

condition of Experiment 1 is congruent with such theorizing, as is the fact that in Experiment 2. patient M.L. maintained the capacity to generate complex mental images given she has an intact left parietal lobe. The finding that M.L. was unable to very successfully rotate three-dimensional images indicates that actual rotation of the internal image is mediated by, though not necessarily localized to, the left temporal region (see Figure 14). Notably, it has been previously shown that damage to the right temporal region alone does not result in any mental rotation impairment (Farah, Hammond, Levine, and Calvanio, 1988), further suggesting that it is uniquely the left temporal lobe (and not the right, nor bilateral engagement of both) that mediates the rotation process.

Throughout Experiment 1, but particularly during mental rotation, a significant activation of the right frontal lobe was in evidence. This activation may be attributable to the frontal lobes responsibility for making comparisons between the images and, subsequently, arriving at a match/no-match decision. Additionally, this finding is consistent with hypothesized executive functioning of the right frontal region during mental rotation, perhaps a byproduct of the well-documented contribution of the frontal cortex to the preplanning and organization of all purposeful action (see Glosser and Goodglass, 1990; Luria, 1973; Pribram and Luria, 1973), especially those involving visual images (Guariglia, Padovani, Pantano and Pizzamiglio, 1993).

It is noteworthy that in many primates, the right frontal lobe is known to be cortically connected to the left inferior parietal lobule and the rostral half of the left temporal lobe (Pandya and Barnes, 1987; Seltzer and Pandya, 1984; Stuss and Benson, 1986; 1987).

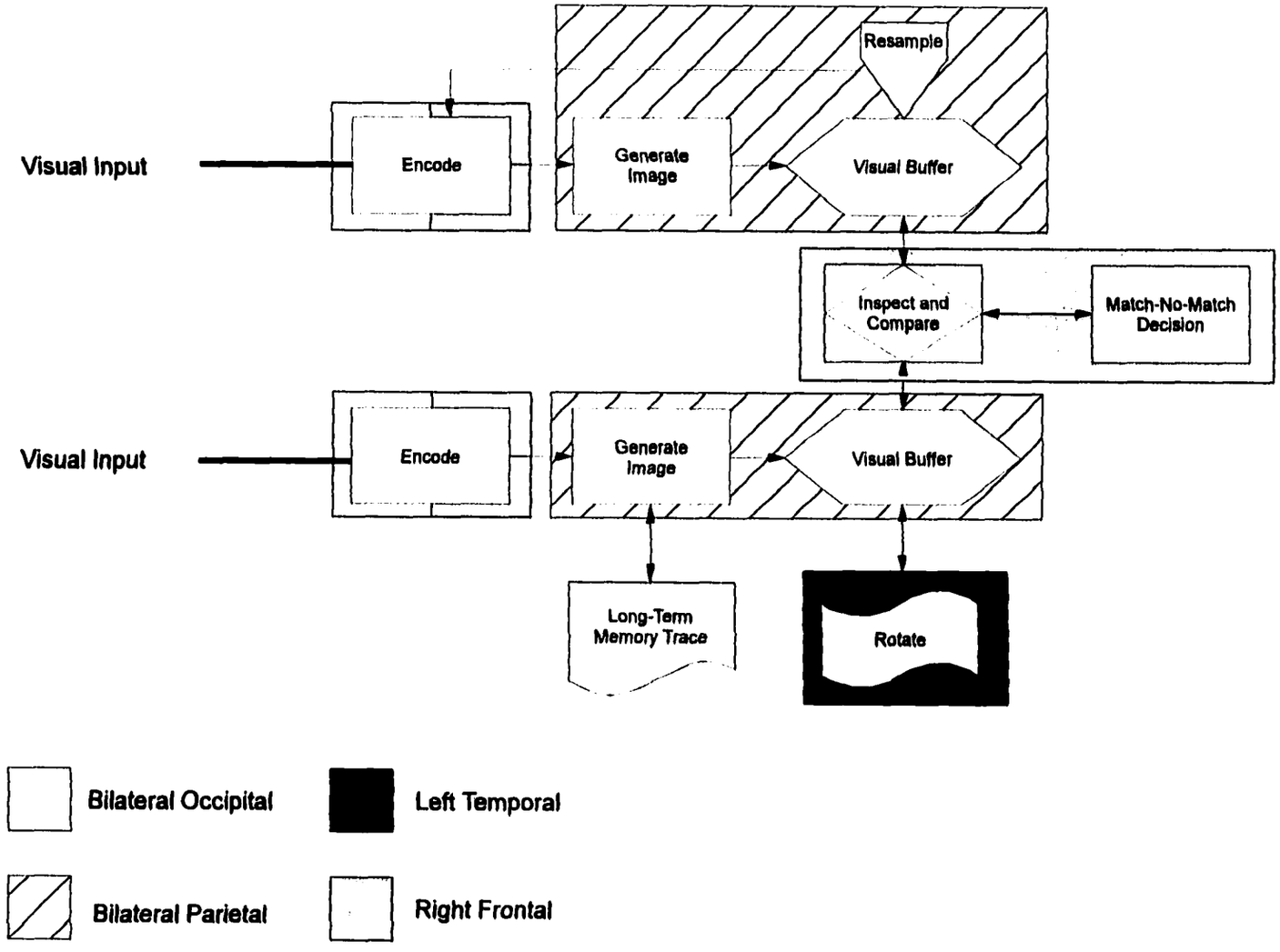


Figure 14: Model of Subcomponent Processes Comprising Mental Image Generation and Mental Rotation

And in humans, it is also connected to V5 (Barbas and Mesulam, 1985). Thus, by way of speculation, it may be through these interconnections that the right frontal lobe exerts its executive control, and has direct access to the information necessary for coordinating the various subcomponents involved in successful mental rotation performance.

Experiment 3 was designed in an attempt to further investigate the brain regions that participate in the internal generation of complex images. One of the fundamental problems with the study of internal image generation is the inability to behaviorally validate that, during the performance of the task, an image is actually being generated. The use of the HIT offered one of the ways to minimize this problem. While participants are observing the inkblot, their subsequent verbal report of what they "see" in the stimulus is not physically present. Thus, these reports must be based on internal representations of images that are being created. As internal image generation may activate similar cortical regions as visual perception, two control conditions were used in Experiment 3 to tease apart the cortical regions responsible for simple visual object and situation processing, contrasted with the extensive image generation required by the HIT.

Consistent with findings of Experiments 1 and 2, activation of the occipital, parietal and frontal regions were also found in Experiment 3 (see Figure 12). As suggested in Experiment 1, the significant activation of occipital and parietal lobes was most likely related to the effort of encoding and maintaining the visually perceived image as well as the spatial relationships of the component parts of the image (potentially also the perceived motion of the component parts) in the visual buffer which was hypothesized to be localized to the parietal lobes. One notable difference in Experiment 3, however, was that there is no

preferential activation of the left parietal lobe as noted in the first experiment. This finding is most likely related to the nature of the stimuli used. Namely, while in Experiments 1 and 2 stimuli were simple line drawings of the three-dimensional stimuli which required a three-dimensional internal image generation (for successful task performance), in Experiment 3 stimuli were much more varied and encompassed drawings of animate and inanimate objects and situations, and virtually limitless possibilities for interpretation exist in HIT. Consequently, it is possible that three dimensional image generation selectively engages the left parietal lobe (see Figure 3), but both parietal lobes mediate image generation and visual buffering process (see Figures 12 and 14).

Again consistent with Experiment 1 and 2 findings, HIT produced an increase in the involvement of the right frontal lobe. As already mentioned, the right frontal lobe and its role during internal image generation and manipulation have previously been implicated in research on various brain damaged individuals (Glosser and Goodglass, 1990; Guariglia, Padovani, Pantano and Pizzamiglio, 1993). Also, given its involvement in organizing and controlling behavior and participation in the decision making processes (Luria, 1973) as suggested in Experiments 1 and 2 , and since repeated images need to be voluntarily recalled from the long term memory and compared/matched to the visually perceived inkblot, the following hypothesis may be constructed.

In the OR and SR conditions, where the task is simple object or situation identification, the required involvement of the frontal lobes (and they are presumably always involved when guided behavior occurs) is minimal, and therefore not in evidence using EEG. However, in the HIT condition, the right frontal lobe becomes essential for task performance.

Namely, while the image of an inkblot is perceived, encoded and maintained in occipital and parietal cortices, that image itself is insufficient as a basis for the type of imagery report that is required from participants. One does not "see" anything in any given inkblot as there is nothing to "see". Thus, a participant must create/activate internal images stored in long-term memory and "find" a best match. This kind of active internal image generation process may be guided by the right frontal lobe much like the mental rotation process was guided by the right frontal lobe in Experiments 1 and 2.

Given that any number of images might be created/activated (i.e., any one inkblot can elicit numerous pictures "seen" in it) the role of the right frontal lobe may be to guide the following complex sequence: (1) eliciting images stored in long-term memory based on the limited information contained in an inkblot, (2) comparing that image to the inkblot encoded while it is being maintained by the occipital and parietal cortices, (3) deciding on the goodness of the likeness, and (4) formulating an actual response (i.e., verbal description of the image with the best likeness to the inkblot).

It should be mentioned that, as for mental rotation, all necessary anatomical connections of the frontal lobe with the hippocampus, inferior temporal, parietal and occipital cortices exist, thus enabling the performance of this complex imagery task (for reviews of frontal lobe connections see Goldman-Rakic, 1987; Van Essen, Anderson and Felleman, 1992; Stuss and Benson, 1986; Perecman, 1987)

While some activation of the temporal regions was expected due to the hypothesized memory storage of visual representations of objects to the inferior temporal regions, it was not registered in Experiment 3. Two possible explanations are that, either the process of

retrieval of visual image from memory is very quick and easy, and thus not reflected in EEG, or the more relevant part of this process is mediated by the right frontal lobe as suggested by the present EEG recordings.

To further investigate the executive and guidance of behavior role of the right frontal lobe, Experiment 4 utilizing a schizophrenic patient was conducted. Individuals suffering from schizophrenia have been reported to have relatively poor responses in the HIT, with a corresponding hypoactivation of prefrontal regions while performing such cognitive tasks (Weinberger, Berman and Zec, 1986). Due to his disorder, the expectation was that the responses of this patient when presented inkblots, would be rated poorer as compared to psychoneurologically normal individuals, and would be accompanied by relatively lesser activation of the right frontal lobe.

Somewhat surprisingly, the activation pattern revealed by the schizophrenic participant in Experiment 4 was remarkably similar to that recorded in normal individuals. Thus, some post-hoc interpretation is required. As Experiment 4 was exploratory in nature and utilized only one patient, these results should be interpreted with caution.

Given that the HIT tasks requires that participants be able to attend to a cognitive task for 20 minutes, a more severely ill individual that is more likely to have a pronounced hypofrontality, would not be able to participate. Conversely, patient D.K. was a remarkably high functioning individual whose behavior was quite appropriate and, aside from some psychomotor slowness and a slight tendency to perseverate, his cognitive abilities appeared well preserved. It is therefore likely that this patient's frontal lobe function was correspondingly also well preserved. As a result, he was able to engage his right frontal lobe

when performing the HIT task which would account for his relatively successful performance. This finding suggests that there is potentially only a narrow window in the progression of schizophrenia in which the frontal lobe function would have deteriorated enough to be detectable in this task performance and EEG recording, but would still be preserved enough to allow the patient to successfully participate in the task. Therefore, it is questionable whether further experimentation with a greater number of schizophrenic participants would be any more revealing.

Overall, the findings of all four experiments conducted here demonstrate that the brain performs complex cognitive tasks like mental imagery and mental rotation by utilizing resources of multiple brain regions organized into a functional system. In the case of image generation and mental rotation, it appears that such mediation areas are located in both cerebral hemispheres and interactively complement one another when engaged in such processing (see Figure 14).

Moreover, the present experiments argue that both occipital lobes are necessarily involved in the stimulus encoding and image generation process, while the parietal lobes subserve mental image generation, and it appears that in particular the left parietal region is involved in generation and maintenance (i.e., the visual buffer) of three dimensional images. The left temporal lobe was noted to be involved specifically in three dimensional image rotation. Consistent with Luria's hypothesizing of the role that the frontal lobes play in organizing preplanned behavior, the right frontal lobe region was shown to be consistently active across all conditions involving complex image generation (and is therefore not apparent in OR and SR conditions of Experiments 3 and 4) and during mental image rotation.

Thus, the above findings, taken in composite, would account for some of the lack of consensus in the literature over which of the two hemispheres is superior in performing mental image generation and/or rotation, as only a componential approach would offer a way of identifying which cortical regions play a role in any given cognitive task. Much of the past research ignored the functional organization of the brain, paying far more attention to hemispheric superiority. As the present results suggest, this is far too narrow an approach if the expectation is better understanding of how brain negotiates tasks of amazing complexity such as mental image generation and rotation.

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